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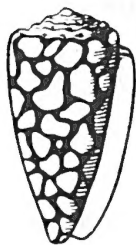
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On the occurrence of the genus *Callocardia* in Australian waters, with the description of a new species

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ABSTRACT

Callocardia thorae, new species, described from twelve dredging stations off the central part of the east coast of Australia between the Capricorn Channel, Queensland and North Solitary Island, New South Wales, represents the first report of the occurrence of the bivalve genus *Callocardia* in Australian waters, and apparently the first south of the Gulf of Siam. The average depth of the species along the east coast is 139 metres.

INTRODUCTION

While viewing the extensive molluscan collections of Mrs Thora Whitehead in Chapel Hill, Brisbane, Queensland, the writer had his attention drawn to an unusual species of Bivalvia that she had not been able to identify. The general shape suggested the genus *Glossus* Poli, 1795, but it lacked the strongly protruding prosogyrate umbones characteristic of that form, and possessed a well-developed, but weakly impressed, pallial sinus and a rather unusual venerid hinge. Subsequent examination of the collections in the Australian Museum in Sydney revealed additional specimens. Comparison with other species in the collection, plus a review of the literature, has lead to the conclusion that the form is a new species referable to the genus *Callocardia* A. Adams, 1864.

So far as the writer has been able to ascertain this is the first record of the genus from Australian waters, and apparently the first south of the Gulf of Siam, from which Lynge (1909: 229) recorded "*Cytherea* (*Caryatis*) *isocardia*, Sow." [= *Callocardia guttata* A. Adams, see discussion below].

The writer is much indebted to Mrs Whitehead for calling his attention to this form and for the gift of specimens and the furnishing of information concerning them and others in her collection.

TAXONOMY

Family VENERIDAE Rafinesque, 1815
Subfamily PITARINAE Steward, 1930
Genus CALLOCARDIA A. Adams, 1864
Callocardia A. Adams, 1864: 307.

Type species, by monotypy: *Callocardia guttata* A. Adams, [= *Cytherea* (*Caryatis*) *isocardia* G.B. Sowerby, 1888 (unnecessary new name for *Callocardia guttata* A. Adams, not preoccupied by *Cytherea guttata* Römer, not described until 1866, *fide* Dall, 1902: 353)] Type locality: Off Quelpaart Isl., Korea 48 fathoms [=88 m.].

"*Caryatis* Römer," G.B. Sowerby, 1888: 213 [non Römer, 1862: 58; substitute name for *Pitar* Römer, 1857 (type: *Venus tumens* Gmelin); not *Caryatis* Hübner, 1816 (Lepidoptera)].

Discussion: *Callocardia guttata* was described by Adams (on the basis of a single left valve) without illustration. Consequently there has been lack of agreement as to the nature of the type specimen. Dall (1890, pl. 10, fig. 5) first provided a drawing by E.A. Smith showing the hinge and outline and Habe (1961, pl. 1, fig. 11) gave one of the exterior made by Prof. Jiro Makiyama. The Dall figure shows a produced anterior end with measurements indicating an umbone near the anterior one-third of the total length, but the Makiyama *in* Habe figure suggests a higher, more rotund outline, with the umbo near the anterior one-sixth of the length. The illustrations of later collected specimens given by Kuroda (1952, text figs. 3, 4; obtained from "40 fathoms (?) in the Bungo Strait) and by Habe (1977, pl. 2, figs. 15, 16; off Asuzaki, Wakayama Pref., Honshu, from "about 150 m. deep") agree more with the Dall drawing relative to the position of the umbones, but the Habe specimen seems to have a distinctly more narrowed and sharply rounded anterior end.

Examination of the type specimen in the British Museum (Nat. Hist) indicates that the Dall figure is more nearly of the proportions of the type specimen than is that of Makiyama *in* Habe, but neither is in complete agreement. As may be seen from the photograph of the type (text-figure 1) the umbo is at the anterior $\frac{1}{4}$ of the length of the specimen.

There has been much uncertainty as to the systematic position of *Callocardia*. Most of it appears to have stemmed from a question as to the presence or absence of lateral teeth. Adams states in his description "*dentis lateralibus nullis*" and, in his discussion, adds: "The complicated nature of what I have termed the anterior cardinal tooth . . . together with the absence of lateral teeth, will distinguish *Callocardia* from the *Isocardia* of Lamarck [= *Glossus* Poli, 1795]." Furthermore, Makiyama's drawing of the hinge of the type specimen gives no indication of a lateral tooth.

The illustration of the hinges given by Smith (1900:81, fig.1), based upon two perfect specimens collected in Hong Kong and originally reported by Sowerby (1888:212), does not, in the words of Jukes-Browne (1913: 340), "clearly bring out the existence of the anterior lateral in the left valve, but Mr Smith informs me that it is there — 'an erect acute tooth rising from the margin of the hinge plate'." Examination of the holotype shows that there is an anterior elongation of the ventral end of the median cardinal that terminates in a small projection (near the lunular margin), which fits into a corresponding pit in the opposite valve, thus functioning as a lateral tooth (see plate 1, fig. 1d).

The unusual nature of the hinge structure, which has been the basic reason for the uncertainty regarding the systematic position of *Callocardia*, was well discussed by Dall (1903: 1237): "It is known from the researches of Bernard that the anterior and posterior teeth of the same valve are originally continuous laminae; thus the superior lamina of the left valve breaks up into the posterior cardinal and the anterior lateral, while the inferior lamina divides to form the two other cardinals of the valve. Ordinarily the primary connections are lost sight of in the adult, and the cardinal teeth appear to spring from an imaginary centre under the hinge-margin above them. In certain groups such as *Callocardia* . . . or *Veneriglossa*, however, the anterior and posterior right cardinals remain connected as well as the anterior and middle left cardinals, and when the valves are closed the former are inserted above the latter and between them and the hinge-margin, while the middle right cardinal fits in below the united pair of the left valve, thus giving an odd look to the hinge, the reason for which requires some study to recognise. As a whole the . . . group represents an earlier type than the typical *Venus* and one with somewhat more archaic hinge characters. Of these *Callocardia* is unquestionably the least developed."

CALLOCARDIA THORAE H.E. Vokes, sp. nov.

Plate 1, figures 1a-d, 2a-c, 3

Description: Shell large for the genus, strongly inflated, almost subspherical in shape, reminiscent of some forms referred to the Glossidae in external appearance and proportions, but having a less deeply excavated lunule margined by a well-developed groove, and strongly inflated, prosogyrate umbones not as gyrate and protruding, but situated between anterior one-third and one-fourth of total length; dorsal valve margin broadly arched, anterior and ventral margins rounded, the anterior more sharply so than the ventral; posterior straight to slightly medially concave as a result of broad, very shallow, postero-dorsal umbonal groove; external surface smooth, marked only by growth lines sometimes forming fine concentric rugae near ventral margin of larger specimens; colour white, with small radially aligned tan to yellowish-brown spots on some valves during earlier growth stages, often as a single row of three or four spots adjacent to posterior dorsal margin — on no specimens examined extending to the posterior or ventral margin, present on the median as well as posterior dorsal surfaces of only one specimen (see fig. 3) and none showing any anterior ones. Remnants of a thin, chalky intritacalx present on all specimens, usually preserved in lunular area under umbones and towards ventral and posterior margins.

Hinge with three cardinal teeth and an anterior lateral tooth in each valve, all borne on a narrow hinge-plate marked by an unusually sinuate, upturned ventral margin; anterior and median cardinals of left valve of a continuous structure, flexed dorsally; anterior cardinal trending vertically and median postero-ventrally; posterior cardinal narrow and linear, separated from median one by a deep socket; anterior and posterior cardinals of right valve also continuous dorsally, posterior one bifid, anterior slender, lamellose and ventrally truncated; continuity between the two thinned, somewhat tenuous above depression, which receives the flexed "hook" connecting the two left cardinals; median right cardinal relatively short, almost a dorso-ventrally elongated narrow nodule, located adjacent to ventral margin of hinge-plate; ventral truncation of anterior cardinal resulting in a sharply rounded continuation of the socket between anterior and median cardinals; this continuation receives the anterodorsally trending upturned margin of left hinge-plate, latter narrower in this area than that of the right valve. Left anterior lateral tooth an erect acute nodule rising immediately dorsal to, and attached to, the upturned ventral rim of hinge-plate; in the right valve a pair of nodes, the larger ventral one erect, rising in a position similar to that of left lateral, with the smaller node projecting from dorsal side of plate into the medially depressed central portion of that structure, the two nodes constricting the depression and forming anterior to them, a pseudo-socket for the reception of the lateral from left valve. Ligament opisthodontic, narrowly elongate, deeply incised between valve margin and hinge-plate with ligament almost completely internal.

Inner margins of valves smooth, slightly thickened ventral to pallial line; pallial sinus not well demarked, broadly triangular with a sharply rounded apex; adductor scars subequal, posterior roundly ovate, anterior narrowly elongate with dorsal end extending onto ventral side of upturned anterior end of hinge-plate; outer sides of both scars very near valve margin.

Holotype, Australian Museum No. C.131238; length 25.6 mm, height 23.2 mm, diameter (paired valves) 20.4 mm; Fisheries Research Vessel "Kapala", 134 metres, 28°13-18'S., 153°53'E., off Danger Point, New South Wales.

Paratype, Australian Museum No. C.131239; length 23.7 mm, height 23.0 mm, diameter (paired valves) 22.3 mm; HMAS "Kimbla", stn. 20: 115 metres, 23° 08.4' S., 152° 12.3'E., 29 km (18 miles) northeast of North Reef, Queensland.

Paratype, Australian Museum No. C.131240; length 28.3 mm, height 25.8 mm, diameter (left valve) 11.5 mm; Fisheries Research Vessel "Kapala", 146 metres, 28° 16-17'S., 153° 50-51'E., East of Tweed Heads, New South Wales.

Discussion: The relatively few specimens of *Callocardia guttata* available make it difficult to give a precise comparison between that form and the present species. *Callocardia thorae* appears to be distinguished from *C. guttata* primarily in being a larger species; the average size of the 7 paired valve specimens, plus 7 left and 4 right valves available for study is: length 24.0 mm, height 21.9 mm, diameter 20.0 mm; the average of the type, plus measurements given in the literature, for *C. guttata* is: length 18.8 mm, height 16.45 mm, diameter (paired valves) 15.1 mm. In addition,

the hinge-plate of *C. thorae* is almost twice as broad, and the pallial line is much closer to the valve margin; the pallial sinus is somewhat broader ventrally, much more sharply rounded at its dorsal extremity and less anteriorly projecting overall.

Distribution: The specimens listed above, which were the basis for the present study, all come from off the central part of the east coast of Australia. The most northern records are from the Capricorn Channel off the central Queensland coast, and the most southern one is of a paired valve specimen dredged by the Fisheries Research Vessel "Kapala" northeast of North Solitary Island, 29° 47-50'S., 153° 38-39'E. The specimens from the twelve stations within this interval came from depths between 115 and 165 metres, with the average depth being 139 m.



Text-figure 1. *Callocardia guttata* A. Adams, holotype BM(NH). Length 18.5 mm, height 17.1 mm; locality, Island of Quelpaart, 48 fathoms.

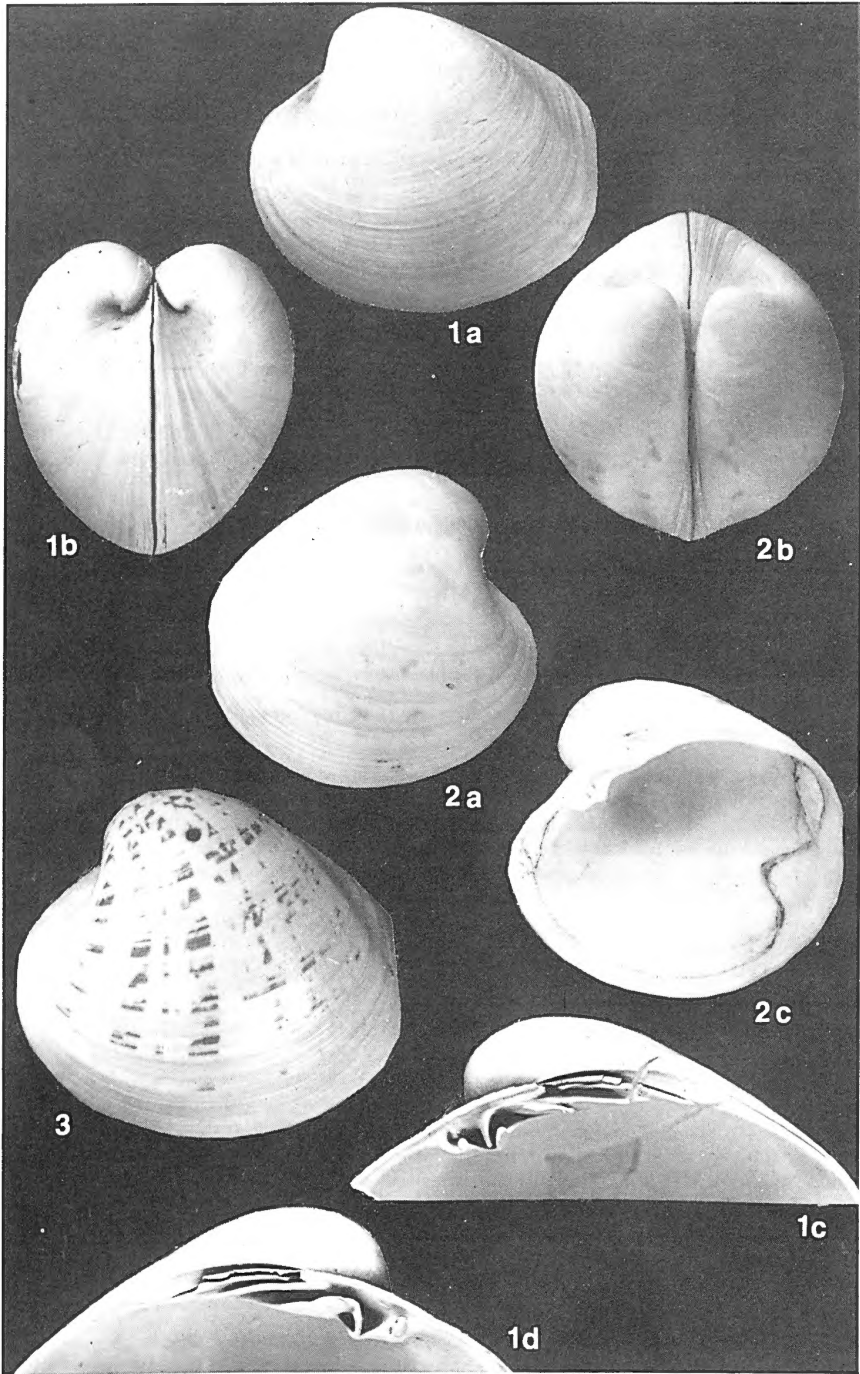
In his discussion of the form from the Gulf of Siam that he identified as *Cytherea* (*Caryatis*) *isocardia* Sowerby (= *Callocardia guttata* Adams — see above) Lyngé (1909: 133) stated: "Though the shell which I have before me . . . differs somewhat in form from the *C. isocardia*, Sow., I can scarcely be wrong in referring it to this species." Unfortunately he did not figure his specimen, but it is to be noted that the dimensions he cites for it, "Long. 26 mm., alt. 22 mm., crass. 20 mm." are more similar to those of the present species, being larger and apparently somewhat more inflated than is *C. guttata*.

If this form should prove to be referable to *C. thorae* the range of this species will be extended considerably to the north.

CALLOCARDIA THORAE H.E. Vokes, sp. nov.

Plate 1

1. Holotype, Australian Museum No. C.131238; la, exterior of left valve, x2; lb, anterior view of paired valves, x 2; lc, hinge of right valve, x 3.5; ld, hinge of left valve, x 3.5. Off Danger Point, New South Wales, depth 134 metres.
2. Paratype, Australian Museum No. C.131239; a proportionately shorter, more obese specimen; 2a, exterior of right valve, x 2; 2b, dorsal view of paired valves, x 2; 2c, interior of right valve, pallial line, pallial sinus and adductor muscle scars delineated before photography, x 2, 29 kilometres northeast of North Reef, Queensland, depth 115 metres.
3. Paratype, Australian Museum No. C.131240; exterior of left valve of largest specimen in collection, and the only one with colour pattern extending on to the median as well as posterior dorsal surface, x 2. Off Tweed Heads, New South Wales, depth 146 metres.



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Analysis of species lineages of some Australian thiarids (Thiaridae, Prosobranchia, Gastropoda) using the evolutionary species concept

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ABSTRACT

The evolutionary species definition is applied to 16 populations of Australian thiarids through the numerical analysis of an electrophoretic data set. Thirteen populations were assigned to a single lineage on the basis of their common evolutionary past and their evolutionary disjunction from the remaining three populations. Members of this lineage were referred to the species *Thiara balonnensis* (Conrad, 1850). The relationships of the other three populations, which were tentatively assigned to *Thiara denisoniensis* (Brot, 1877), were uncertain apart from being outside this lineage.

INTRODUCTION

A fundamental barrier to the natural (*sensu* Gilmour, 1961) classification of the Thiaridae is presented by the parthenogenetic mode of reproduction found in many species (Jacob, 1957a & b). Asexually reproducing organisms may produce patterns of variation which are confusing to taxonomists and in general, their delimitation into species falls outside the limits of the biological species concept of Mayr (1963). As asexual reproduction does not permit recombination or reassortment of genes, numbers of apparently independent characters will show a close association within a clone. This will frequently lead to the production of distinctive forms which may be quite dissimilar to other clones, resulting in the recognition of a clone as a named species. A more appropriate classification of distinctive clones may become apparent if many clones are compared simultaneously. However, the criteria to be used in this classification can obviously not be based on reproductive isolation. We require a species concept which is relevant to asexual reproduction.

Wiley's (1978) modification of Simpson's (1961) evolutionary species concept stresses the relevance of the process of speciation to species definitions and provides the most appropriate framework

for the taxonomy of asexual organisms. Here, a species is defined as "a single lineage of ancestral-descendant populations which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate" (Wiley, 1978, p18). Although Simpson's (1961) earlier definition had been criticised for its lack of operationalism (Fritts, 1962; Sokal and Crovello, 1970), Wiley's implied criterion of evolutionary disjunctions between species (Wiley, 1981) seems well suited to the application of numerical methods used in the estimation of evolutionary lineages.

Ideally, the construction of lineages should employ a large number of phenotypic characters, and in particular, those characters which are able to be related directly to the genotype. While it is rarely possible to weigh changes in phenotypic characters in a precise quantitative relationship with their corresponding genotypic changes, it would be wrong to ignore the parameters of the genotype-phenotype relationship entirely. This would invite disproportionate influence of a few characters on the resultant phylogeny estimate. A working compromise is to select a set of characters which are likely to have equivalent amounts of genotypic evolution implied by their changes in state. In this case, similarities in the ontogeny, non-genetic components, and coding of characters should be used in the choice of characters.

Avice (1974) lists some advantages of electrophoretic characters over morphological, or anatomical, characters in the above respect, the most important being their equivalent amounts of genotypic information. Electrophoretic characters were used here, as in terms of genotypic change it is easier to relate a change in allozyme state of one enzyme to that of another enzyme than to compare, say a change in shell length with one of shell sculpture. This does not imply that electrophoretic data will be inherently superior to morphological data in systematic inference. Rather it is the ease with which these data are interpreted which recommends them (see Mickevich and Johnson, 1976, p 268, for a discussion of "data" versus "ease").

Australian thiarids have been referred to a large number of named forms (Iredale, 1943), frequently on the basis of a few morphological characters, and frequently to forms with very limited distribution. The single study which has attempted to compare a number of these "species" (Blackwell, 1969) was unable to reach a definite conclusion as to their validity and preferred to lump them into a single taxon. This situation is symptomatic of thiarids worldwide, and a study by Reich (1937) synonymised a large proportion of the 114 named species treated by him. This apparent overnaming suggests that the application of the evolutionary species concept to thiarids may prove most effective.

This study analyses relationships within a set of 16 Australian thiarid populations. Electrophoretic characters are used as the basis for an assessment of overall similarity between the clones of these populations, i.e. a phenetic classification, and to reconstruct the evolution of these forms, i.e. a phylogenetic classification. This allows both the assessment of their present relationships and the examination of the likely pathways which lead to these relationships. In this way, it should be possible to detect any disjunctions in their evolution.

MATERIALS AND METHODS

Sample material: Fourteen localities were chosen for inclusion in this study such that certain subsets of the 14 represented a) an extensive geographic range within Australia, b) a contiguous, or nearly so, distribution, c) morphologically distinct populations, and d) a wide range of habitats. Sample localities (Fig. 1) followed in parentheses by 3-letter codes and the catalogue numbers of voucher specimens lodged at the Western Australian Museum were: Lake Leschenaultia (LES : 471-80), Swan River (MSW : 680-79), Ellendale Pool (ELT : 461-80 & ELM : 465-80), Fortescue Falls (TFT : 469-80 & DFT : 466-80), Fitzroy River (FIZ : 459-80) and Ord River (KUN : 457-80) all of Western Australia; Victoria River (VIC : 458-80) and Finke River (FIN : 470-80) of the Northern Territory; Brisbane River (BAL : 463-80) and Tinaroo Dam (STA : 464-80) of Queensland, and Lake Liddell (LID : 460-80) in New South Wales. Exact locality data are given in Stoddart (1980).

Only at two sites were there more than a single morphotype apparent. At these sites, several shell characters showed clearly bimodal distributions (Stoddart, 1980) and as morphotypes from each site were initially referred to different named forms, snails were subdivided into populations on this basis (viz. ELT/ELM and TFT/DFT).

Using existing specific classifications based on shell characters and the generic scheme of Pace (1973) and Stoddart (1980) the 16 populations were referable to six taxa on the basis of the comparisons with descriptions and figures of types:

- Thiara (Thiara) balonnensis* (Conrad, 1850) — BAL, LID
 Type locality — Balonne River, Australia
T. (T.) tetrica (Conrad, 1850) — FIN, CPM
 Type locality — Murray River, S.E. Australia
T. (T.) australis (L. & H. Lea, 1850) — KUN, VIC, MNP, TFT, FIZ
 Type locality — Victoria River, Northern Territory
T. (T.) incerta (Brot, 1862) — MSW, LES, ELT, MUR
 Type locality — Avon River, Western Australia
T. (Melanoides) denisoniensis tacita (Iredale, 1943) — STA
 Type locality — Cardwell, Queensland
T. (M.) d. ultra (Iredale, 1943) — ELM, DFT
 Type locality — Clarence River, New South Wales.

Type localities given for many of the species of Australian thiarids are often vague and sometimes misleading. For example, the species *denisoniensis* (Brot, 1877) has Port Denison, Qld as its given locality, even though this is a marine embayment and more likely to be the port where specimens were loaded onto a ship, rather than where they were found. Others are from rivers which stretch for hundreds of kilometres. Thus it is extremely difficult to be certain whether snails were collected from type localities. Of the present populations, VIC and MSW were collected from the same river systems as the types of their assigned species. With the exception of ELM and DFT, other populations occurred in the same broad geographic region as the types of their assigned species.

Electrophoresis: Horizontal starch gel (12% Electrostarch, Otto Hiller & Co, Lot 307) electrophoresis was performed using refrozen foot tissue homogenised the previous day. Snails were frozen and stored at -20°C for between 1 day and 6 months prior to being homogenised. Controls indicated no apparent effects of freezing or storage on banding patterns. Gels were stained for the following enzymes: esterase (EST), leucyl-glycylglycine peptidase (LGG), leucyl-proline peptidase (LP), leucyl-tyrosine peptidase (LTY), glutamate oxaloacetate transaminase (GOT), leucine aminopeptidase (LAP), nucleoside phosphorylase (NP), phosphoglucomutase (PGM), 6-phosphogluconate dehydrogenase (6PGD), malate dehydrogenase (MDH), mannose phosphate isomerase (MPI) and superoxidase dismutase (SOD). All 4 LGG bands correspond to bands with identical mobility in LTY and were presumed to result from non-specific allozymes, that is, enzymes which metabolise a number of different substrates. Each allozyme was scored as a single character.

Confident interpretation of banding patterns into locus-allele models relies on determining patterns of inheritance of bands from breeding experiments. As this was not possible for an obligate parthenoform, each band was considered a discrete character and scored on a presence/absence basis. Bands were labelled alphabetically in order of decreasing anodal mobility.

Numerical methods:

1) *Phenetic:* Presence/absence characters were used to compute a matching coefficient of similarity, Jaccard's S_j (Sneath & Sokal, 1973). This measure of overall similarity was then used in the UPGMA algorithm (Sokal & Michener, 1958) to sequentially cluster the populations and produce a phenogram showing their relationships.

2) *Phylogenetic:* An unrooted Wagner tree (Farris, 1970), or network, was computed using the Wagner78 program of Farris, run on the Western Australian Regional Computing Centre's Cyber 76. Wagner methods are a form of cladistic analysis which attempt to specify the evolutionary pathway between a series of taxa by searching for the path requiring the least amount of evolution. Essentially this means that path which minimises the number of times any character is derived, i.e. the parsimony criterion (Felsenstein, 1983). The distance between each taxon on the tree is called the patristic distance and was defined as the total number of divergent, convergent and parallel evolutionary steps between each, with minimal estimates of the latter two produced under the parsimony criterion.

RESULTS

After correcting for non-specific enzymes, 46 scoreable characters remained (Table 1). No variation in banding pattern was seen within any population, suggesting that each contained only a single clone of genetically identical snails. With the exception of the MSW-LES pair, no two populations shared the same clone. The LES population occurs in a man-made empoundment and is almost certainly derived from snails originating from the same river as MSW. Differences between clones were extensive with Sj's from 0.98 to 0.55 (Table 2).

The topologies of the phenogram (Fig.2) and Wagner tree (Fig.3) are largely concordant. Both show that for the majority of populations, electrophoretic estimates of genetic distance are similar to amounts of geographic separation. When DFT, ELM and STA are excluded, both Sj and patristic distance (PD) are significantly correlated with differences in latitude between populations (Table 3). Both correlations become nonsignificant on inclusion of DFT, ELM and STA, and predictions of genetic distances between these and the other thirteen populations, using the relationship derived above, typically underestimate the actual values. Regression statistics are shown in Table 3.

DISCUSSION

A necessary corollary to the search for an evolutionary disjunction between lineages is that there must be an ordered element to evolution within a lineage. Such an element has been previously reported for this group in the context of the evolution of an asexual organism (Stoddart, 1983). It is seen here in the relationship between a geographic parameter (latitude) and genetic distance measures (Sj and PD). Presumably this reflects the influence of the dispersal process on the time elapsed since clones shared a common ancestor (Stoddart, 1983). Thus for the 13 populations where this relationship holds, a common evolutionary tendency is apparent in that there has been no substantial alteration of characteristics affecting evolutionary response. Included here are such features as generation time, ploidy and niche. The breakdown of this relationship when STA, DFT and ELM are included and the extent of genetic differences between these and the other 13 suggest the presence of an evolutionary disjunction between the main lineage and these three clones.

At each site, new clones will be produced by mutation with subsequent competition between these and extant clones resulting in a reduction in clonal diversity (Jaenike *et al.*, 1980). Additionally, Livshits and Fishelson (1983) show that some populations of *Thiara tuberculata*, a species previously thought to be entirely parthenogenetic, reproduce sexually. Patchy occurrences of sexual reproduction, whether temporally or spatially patchy, will also generate new clones in apparently asexual species of thiariids. The number of clones present at each site will depend then on the balance between the rate of viable mutations, or the frequency of sex, and the intensity of interclonal competition. The uniclonal nature of most sites suggests the rate of clonal production to be lower than the rate of clonal extinction. Thus for two clones to persist in time they must be geographically separated or occupy largely non-overlapping niches. Clones of the main lineage provide an example of the former category and the ELM-ELT and DFT-TFT clone pairs an example of the latter. The sympatric occurrence of these latter clones strengthens the previous conclusion that members of each pair belong to separate lineages (species), thus having distinct niches and divergent evolutionary tendencies.

It is not the sympatric occurrence of ELM and DFT with members of the main lineage that alone dictates their separation from this lineage. Rather, it is their disjunction from the genetic-geographic association characterising the main lineage. It would be possible for two clones to exist sympatrically and be quite distinct, yet to be referable to a single lineage when compared with adjacent members of that lineage. Similarly, while no members of the main lineage occur sympatrically with STA, this population can still be separated from this lineage on the basis of its much greater genetic distance from members of the lineage than that predicted from its geographic position.

Thirteen populations, LES, MSW, ELT, MUR, CPM, MNP, TFT, FIZ, KUN, VIC, FIN, BAL and LID, then may be assigned to a single species. By virtue of priority of publication the name for this species should be *Thiara (T.) balonnensis* (Conrad, 1850), this being the most senior of the four

names represented by this group. Although neither BAL nor LID, the populations originally referred to *T. balonnensis* on morphological grounds, are from this species' type locality, it seems unlikely that a population which occurs not far from these two and is so similar morphologically would form part of a separate lineage. Asexual groups are conservative with respect to speciation (Stanley, 1979) and further study may show *T. balonnenis* to be conspecific with a more cosmopolitan species such as *T. scabra* or *T. tuberculata*. However, the appropriate answer to this question requires the comparison of series of populations from all three species.

Of the taxa not included in the *T. balonnensis* lineage, both phenogram and Wagner tree suggest a taxonomic separation of STA from DFT and ELM in excess of the subspecies level produced by Iredale (1943). This is apparent in the substantial genetic distance between these two groups, vis-a-vis distances between members of the main lineage. However, further populations of these species are needed to clarify their status by determining if they are part of a single lineage or not. Although it is certain they are not conspecific with *T. balonnensis*, there is insufficient information to comment on their placement in a separate subgenus. In the absence of substantive evidence, these forms are left in the taxa to which they have been assigned already.

Although the application of the evolutionary species definition is cumbersome because series of populations are needed to discern lineages, it is preferable to taxonomic criteria based on reproductive isolation. In the present context it has demonstrated its utility by showing that order exists within a set of phenotypically disparate populations in a troublesome group. Its use for the parthenogenetic thiarids may remedy the apparently gross overnaming of species which has stemmed from an inability to deal with discrete clonal variation.

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TABLE 1. Clonal structure of the 16 study populations. Each letter denotes the presence of that band in a clone. Bands appearing for both LTY and LGG were LTY, a,d,f and h. N is the sample size in each case.

	Clone	N	Enzyme										SOD
			LTY	LP	LAP	EST	MPI	PGM	6PGD	MDH	NP	GOT	
1.	MSW/LES	40/15	adehf	bc	acd	bdegh	bcd	adehg	abc	cd	a	a	ab
2.	ELT	10	adehf	bc	acd	abdegh	abcd	abdehf	abc	bd	a	a	ab
3.	MUR	20	adehf	bc	acd	bdegh	acd	abdehg	b	bd	a	a	ab
4.	LID	9	adehf	bc	cd	bdegh	ac	befg	ab	de	a	a	ab
5.	CPM	10	adehf	bc	acd	abdegh	acd	bdehg	bc	abcde	a	a	ab
6.	MNP	10	adeh	bc	ac	abdegh	acd	bdef	bc	bc	a	a	ab
7.	TFT	6	adeh	bc	ac	abdegh	acd	bdf	ac	abcde	a	a	ab
8.	BAL	10	adeh	bc	ac	bdgh	ac	befg	c	abcde	a	a	ab
9.	FIN	10	ah	c	ac	adehg	ac	bcefg	b	abcde	a	a	ab
10.	VIC	8	adeh	a	c	abdegh	ac	bef	bd	bd	a	a	ab
11.	KUN	26	abeh	a	c	adgh	ac	bef	ac	bd	a	a	ab
12.	FIZ	6	abeh	a	c	adgh	ac	bcef	ab	bd	a	a	ab
13.	ELM	8	bdfigh	c	bc	adgh	ab	bg	ab	bde	a	a	ab
14.	DFT	12	bdfigh	bc	bc	dgh	ab	bd	abc	bde	a	a	ab
15.	STA	4	acdgh	a	bc	bcdfigh	a	abdf	d	abde	a	a	ab

TABLE 3. Regression statistics for the relationship of genetic and geographic distance, of the form $Y = bX + a$, where X is the difference in latitude between populations (standardised by division by the grand mean).

Clones in the Regression	Y	a	b	r	R ²
All - (ELM, DFT, STA)	S _j	.87	-.24	-.57*	.32
All	S _j	.78	-.14	-.24	.06
All - (ELM, DFT, STA)	PD	8.08	28.5	.67**	.45
All	PD	16.3	19.0	.32	.09

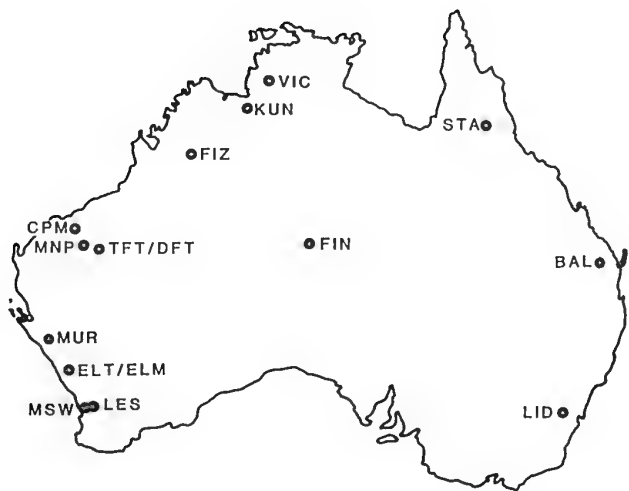


Figure 1: Map of Australia showing the sample sites.

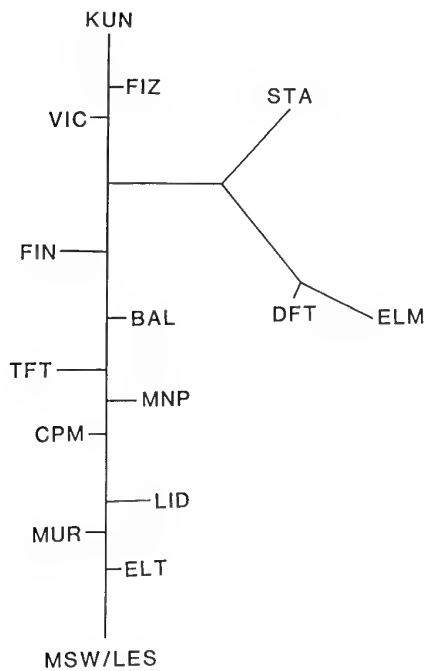


Figure 2: Phenogram resulting from UPGMA clustering based on S_j values.

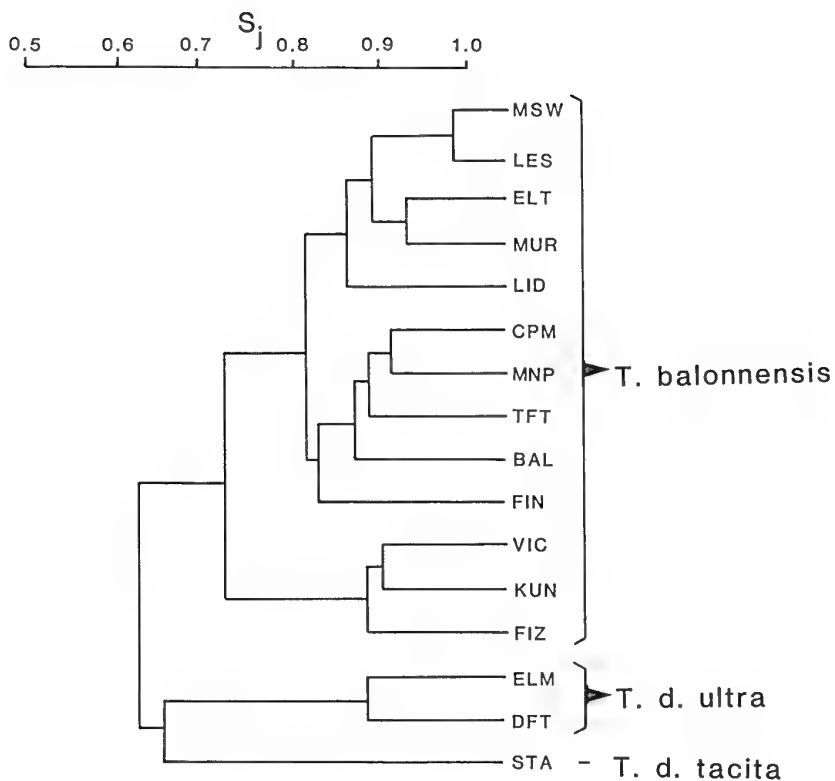


Figure 3: Unrooted Wagner tree. Internode distances are proportional to patristic distances.

Egg masses of three gastropods, *Kerguelenella lateralis* (Siphonariidae), *Laevilitorina caliginosa* and *Macquariella hamiltoni* (Littorinidae), from Macquarie Island (sub-Antarctic).

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ABSTRACT

The egg masses of three species of sub-Antarctic gastropods (*Kerguelenella lateralis*, *Laevilitorina caliginosa* and *Macquariella hamiltoni*) are described. Each species has non-pelagic development in the egg-masses and the relationships of this reproductive strategy to geographical position and egg size are discussed.

INTRODUCTION

The modes of larval development and the reproductive cycles of a number of molluscs and echinoderms from the sub-Antarctic Macquarie Island (54°38'S 158° 53'E) have been previously described (Simpson, 1977, 1982). The egg masses of two gastropod species, *Kerguelenella lateralis* and *Macquariella hamiltoni*, were found during those studies. For a third species, *Laevilitorina caliginosa*, a prediction of non-pelagic development via the laying of an egg mass was made from the number and size of ova in the ovaries of preserved specimens (Simpson, 1977). A subsequent visit to Macquarie Island confirmed the prediction. The egg masses of these three species are described here.

Marine benthic invertebrates in high latitudes have a tendency towards a non-pelagic mode of larval development (Thorson, 1950; Mileikovsky, 1971; Simpson, 1977; Jablonski and Lutz, 1983). The most favoured hypothesis to explain this trend is that slow development rates of larvae in cold water, together with the limited period of seasonal production of phytoplankton food, make it difficult for planktotrophic larvae to complete their development. (However, Clarke (1982) has suggested that slow development rates of invertebrates in polar latitudes have evolved to allow release of advanced, competitive young — as an adaptation to the pattern of food supply to the benthic marine environment. That is, slow development is not the direct result of low temperature.)

Non-pelagic modes of larval development in high latitudes have also been related to: harsh conditions in surface waters for larvae, increased predation for slower developing larvae, availability of suitable substrate for larval settlement, the connection between greater variability in survival of early growth stages and the K- model for reproductive strategy, and decrease in adult size. Further data on the modes of larval development of marine invertebrates across all latitudes will assist the interpretation of the above trend. As Picken (1979) noted, the majority of records are from the northern hemisphere. The southern hemisphere presents a different suite of physical, climatic, and biogeographical factors for any biological phenomenon acting across a latitudinal gradient. Consequently, additional data from the southern hemisphere are especially valuable to elucidate any shift in emphases resulting from components of these factors.

Apart from contributing to the specific objective of obtaining further information to aid in the interpretation of Thorson's Rule, the descriptions of the egg masses of these three species simply add to the knowledge of the life history of the animals. Such information can then be used in future comparisons, whatever the reason, within and across taxa.

METHODS AND COLLECTION SITES

Over a one year period, monthly collections of a number of molluscs and echinoderms were made from the littoral and sublittoral zones of Macquarie Island for the purposes of determining reproductive cycles (Simpson, 1977, 1982). During this time, egg masses of the siphonariid limpet, *Kerguelenella lateralis*, and the littorinid, *Macquariella hamiltoni*, were collected towards the end of the one year collecting period (in the late spring/summer of 1968-69). During subsequent visits to Macquarie Island (in the late spring/summer of 1979/80 and late spring of 1981), further collections of egg masses of these two species were made. Also, during the two latter trips, egg masses of the littorinid, *Laevitorina caliginosa*, were found and collected. All collections were preserved in Baker's formol-cobalt-calcium (Simpson, 1977).

Egg masses were not observed being laid. However, the following indirect evidence provides sufficient assurance that egg masses have been correctly assigned to each species. For *K. lateralis*: this is the only siphonariid on Macquarie's shores. Further, egg masses were collected from rock surfaces inhabited by no other gastropod species. For *M. hamiltoni*: as mentioned in Simpson (1977), egg masses were taken from red algae on which only adult *M. hamiltoni* were present. Also, the confined spaces of many of the sites of the deposited egg masses (at the bases of multi-branched stipes) infer that the layer was a small mollusc. For *L. caliginosa*: the egg masses were collected from rock surfaces on which adult *L. caliginosa* were abundant. The only other gastropod molluscs in the vicinity were *K. lateralis* and the limpet *Nacella (Patinigera) macquariensis*. A third littorinid species is known from Macquarie Island — *Macquariella macphersonae* (Dell, 1964). Adult littorinids were collected at the same time as the egg masses from both the algae and the rock surfaces. No specimens of *M. macphersonae* were found in those collections of adults.

K. lateralis is the dominant organism of one of the prominent zones on the rocky shores of Macquarie Island — the "Bare" Zone, located in the middle region of the eulittoral zone (Kenny and Haysom, 1962; Simpson, 1976). (The term "Bare" designates a zone lacking in macroscopic algae, which dominate the remaining parts of the shore.) Within this zone, egg masses of *K. lateralis* were found, often deposited in shallow crevices and channels. *L. caliginosa* extended high into the eulittoral zone where it is usually found in pools or on the under-surfaces of rocks. Egg masses of *L. caliginosa* were taken from rock surfaces in these habitats. Egg masses of *Macquariella hamiltoni* were found on red algae, particularly *Rhodymenia* sp., at the bottom of the eulittoral zone. The egg masses were predominantly located towards the bases of the algal fronds. The vertical range of *Macquariella hamiltoni* is from the upper sublittoral to the lower eulittoral regions where they are most commonly found attached to red algae.

RESULTS

Table 1 lists the data for the sizes of the egg masses and the eggs, and for the number of eggs per egg mass, of all three species. The data are taken only from egg masses that were collected whole and undamaged.

Figure 1 shows lateral and dorsal views of an egg mass of *K. lateralis* and a late stage embryo, prior to hatching. Figure 2 shows dorsal views of egg masses of *L. caliginosa* with embryos at early and late stages while Fig. 3 shows the same for *M. hamiltoni*. The egg masses of *M. hamiltoni* were deposited in a single layer while those of *L. caliginosa* were laid in a round hump with some eggs overlying others.

For *K. lateralis*, egg masses often had a number of compartments with no eggs in them (see Fig. 1) and these were not included in the above calculations. The number of empty compartments per mass ranged from 0 to 11, with only one egg mass having no empty compartments. There were also empty compartments in the egg masses of *L. caliginosa* and *M. hamiltoni* but far fewer than were found for *K. lateralis*; that is, there were empty compartments in 60% of the masses of *L. caliginosa* (ranging from 1 to 6) and in 35% of the masses of *M. hamiltoni* (ranging from 1 to 5). Again, these empty compartments were not used in the calculations of number of eggs per mass.

The number of eggs per mass showed considerable variation in *K. lateralis* and *M. hamiltoni* but a component of this variation was due to low scores of number of eggs in masses having high numbers of empty compartments.

L. caliginosa lays a larger egg mass than *M. hamiltoni* with a higher number of eggs per mass; the sizes of the eggs in the two species are similar.

DISCUSSION

Typically, members of the Family Siphonariidae lay a benthic egg mass from which planktonic veligers hatch (Berry, 1977). Pelagic egg masses have been described for two south-east Australian species of *Siphonaria*: *S. virgulata* (Creese, 1980) and *S. tasmanica* (Quinn, 1983). (*S. virgulata* has since been designated as a geographical variant of, and hence synonymous with, *S. funiculata* (Jenkins, 1981)). From these pelagic egg masses, the larvae hatch as planktonic veligers. A non-pelagic development to a juvenile stage within the egg mass has been recorded previously in two species: the tropical *Siphonaria kurracheensis* (Thorson, 1940) and the sub-Antarctic *Kerguelenella stewartiana* (Knox, 1955).

The egg masses of *K. lateralis* are very similar to those described for *K. stewartiana* by Knox (1955) — that is, a tough, gelatinous, transparent mass containing a number of compartments (cocoons). The egg masses and a fully developed embryo of *K. stewartiana*, as illustrated by Knox (1955), are shown in Fig. 4 for comparison. The eggs of *K. lateralis* appear to be slightly smaller than those of *K. stewartiana* ($1.26 \text{ mm} \pm 0.27 \text{ S.D.}$ in *K. lateralis* vs. a range of 1.35 — 2.00 mm in *K. stewartiana*). However, the egg measurements of *K. lateralis* did not include the housing compartment which was apparently included in the measurements for *K. stewartiana* by Knox (1955). This would increase the dimension by approximately 0.2 mm. Also, *K. lateralis* had a greater number of eggs per mass ($24.3 \pm 10.2 \text{ S.D.}$ vs. 9 to 35) (Knox (1955)) gave two ranges for eggs per egg mass: 9 to 35 and 12 to 25); however, this may simply be related to the smaller sizes of *K. stewartiana* (maximum length 15.5 mm), compared to those of *K. lateralis* (maximum length 20.8 mm) from the two study areas. From these records, *K. stewartiana* appears to be a slightly smaller species than *K. lateralis*. The similarities in the reproductive modes of the two species are very striking: the reproductive strategy itself, the structure of the egg mass, and the external appearance of the embryo prior to hatching. These similarities indicate that a closer examination of *K. lateralis* and *K. stewartiana* would be worthwhile to verify whether they are two separate species.

These two species of *Kerguelenella* conform to "Thorson's Rule" — the tendency towards a non-pelagic mode of larval development for those members of a taxonomic group that inhabit high latitudes. *S. kurracheensis*, being a tropical siphonariid with non-pelagic development, goes against the trend. However, these three siphonariid species live in, or extend into, the high littoral and it is tempting to suggest that non-pelagic development may have some adaptive advantage for siphonariids occupying this part of the shore. However, such simple correlations are invariably offset with contrary examples, as has been found in other groups — e.g. Littorinidae (Mileikovsky, 1975).

From comparisons with data for other Siphonariidae there is a predictability between egg size and mode of larval development; that is, large eggs (>0.35 mm) indicate non-pelagic development while below that size indicates pelagic development (Table 2). Also, with smaller eggs there are many more eggs per mass. Differences in the size of the egg mass and the corresponding number of eggs per mass for any species would be largely due to different sizes of the spawning parent, as was shown for *Siphonaria denticulata* by Creese (1980).

As previously reported (Simpson, 1977), the egg masses of *K. lateralis* were often invaded by oligochaete worms, particularly in the upper parts of the siphonariid's range. However, the empty compartments of *K. lateralis*, and of the two littorinid species, reported here had no macroscopic organisms within the egg masses. The empty compartments could have resulted from more subtle invasion or predation by micro-organisms, or from the molluscs' failure to deposit an egg into an egg compartment.

Many species of Littorinidae inhabit the highest regions of the littoral zone where there are likely to be special adaptations for reproduction in the harsh, aerial conditions. In a review of larval development in the Littorinidae, Mileikovsky (1975) found that associations could be drawn for ovoviviparity in the littoral fringe (called "supralittoral" by Mileikovsky) and for non-pelagic development via benthic egg masses in the eulittoral zone (called "littoral" by Mileikovsky); however, pelagic larval development occurred in littorinid species from all parts of the shore. Mileikovsky rejected the previously held concept of obligate interrelationships between definite types of larval development in marine benthic invertebrates and their existence in definite ecological zones on the shore. The two species of littorinids in this study occupy wet habitats. *L. caliginosa* extends up to the top of the eulittoral zone but its habitats are pools or the undersurfaces of boulders. The findings provide two further instances of non-pelagic development in a group that exhibits a variety of reproductive strategies.

Both *L. caliginosa* and *M. hamiltoni* are small molluscs, *L. caliginosa* being the slightly larger of the two (5.0 mm maximum length vs 4.0 mm for *M. hamiltoni*). The larger egg mass and the greater number of eggs per mass for *L. caliginosa* may be due simply to its larger size. However, this does not necessarily mean that *L. caliginosa* has a greater fecundity. *M. hamiltoni* may lay more egg masses per individual than *L. caliginosa*.

Comparisons with data for other Littorinidae show a relationship between egg size and pelagic vs non-pelagic development as is the case in the Siphonariidae: large eggs indicate a totally non-pelagic development and small eggs indicate pelagic development (Table 3). Such a relationship apparently results from the greater amount of yolk required for the embryo to reach a crawling, juvenile stage.

For all three species, egg masses were collected throughout the spring-summer period. During that time, egg masses were found with stages ranging from undifferentiated eggs to shelled embryos. Whether egg masses were laid at other times of the year for the littorinids is not known. Egg masses of *K. lateralis* were observed at other times of the year but no collections were made then. The presence of mature ova and spermatozoa in the three species throughout the year (Simpson, 1977) suggests that egg-laying is continuous although it may be held over during some parts of the year.

A likely consequence of non-pelagic development is restricted dispersal resulting in a narrow geographical range. However, *K. lateralis* and *L. caliginosa* have a wide circum — Southern Ocean distribution and *M. hamiltoni* has been found at Heard Island (Dell, 1964). For *K. lateralis* and *L. caliginosa*, the egg masses are firmly cemented to the rocky substrate and the chances of these

egg masses being washed into the sea are extremely remote. Egg masses of *M. hamiltoni* could become sea-borne on dislodged algae. Adults of many species may be rafted around the Southern Ocean on dislodged, floating kelps. Arnaud (1974) listed many invertebrate inhabitants of the kelps of the Kerguelen Islands and proposed that the kelps acted as a dispersal agent for many sub-Antarctic marine invertebrates. *L. caliginosa* and *M. hamiltoni* have been recorded as commonly occurring in the holdfasts of *Durvillea antarctica* (Kenny and Haysom, 1962; Simpson, personal observations) and *L. caliginosa* has been recorded on *Macrocystis* sp. at South Georgia (Arnaud and Bandel, 1978). The wide geographic range of *K. lateralis* is somewhat puzzling as this species has not been recorded as occurring on such kelps.

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TABLE 1. Egg masses (dimensions and numbers of eggs) and egg sizes — for *K. lateralis*, *L. caliginosa* and *M. hamiltoni*.

Egg mass dimensions:			
	n	Mean length, mm (±S.D.)	Mean width, mm (±S.D.)
<i>K. lateralis</i>	33	5.4 (±1.1)	4.6 (±0.9)
<i>L. caliginosa</i>	30	2.2 (±0.5)	1.8 (±0.3)
<i>M. hamiltoni</i>	17	1.9 (±0.4)	1.5 (±0.4)
Eggs:			
Egg masses		No. of eggs per mass	
	n	Range	Mean (±S.D.)
<i>K. lateralis</i>	21	13-55	24.3 (±10.2)
<i>L. caliginosa</i>	20	9-19	12.2 (±2.5)
<i>M. hamiltoni</i>	16	2-9	6.0 (±2.2)
		Eggs Measured	
		Mean diameter*	
		n	mm (±S.D.)
		77	1.26 (±0.27)
		45	0.50 (±0.06)
		29	0.54 (±0.12)

* If egg oval, largest diameter always measured.

TABLE 2. Number of eggs per mass, egg sizes, and ecological mode of embryonic development in some Siphonariidae.

Species	No. of eggs per mass	Egg diameter (μm)	Mode of development	Source
<i>Kerguelenella stewartiana</i>	9-35	1,350 - 2,000	Non-pelagic	Knox, 1955
<i>Kerguelenella lateralis</i>	13-55	1,260 \pm 270 SD	Non-pelagic	This paper
<i>Siphonaria kurracheensis</i>	Hundreds	380 - 500	Non-pelagic	Thorson, 1940
<i>Siphonaria virgulata</i> (= <i>S. funiculata</i>)	9,200	100	Pelagic	Creese, 1980
<i>Siphonaria denticulata</i>	12,200-26,800	100	Pelagic	Creese, 1980
<i>Siphonaria tasmanica</i>	Thousands*	94.9 \pm 6.1 SD	Pelagic	Quinn, 1983
<i>Siphonaria japonica</i>	Thousands*	87 - 91	Pelagic	Abe, 1940

*Inferred from illustration.

TABLE 3. Egg sizes and ecological mode of embryonic development in some Littorinidae.

Species□	Egg diameter* (µm)	Mode of development	Source
Pelagic development:			
<i>Nodilittorina pintoado</i>	60 - 70	Spawned as eggs	Struhsaker, 1966
<i>Nodilittorina picta</i>	70 - 80	Spawned as eggs	Struhsaker, 1966
<i>Nodilittorina acutispira</i>	75 - 93	Spawned as eggs	Underwood and McFadyen, 1983
<i>Littorina zigzac</i>	80	Spawned as eggs	Lebour, 1945
<i>Littorina neritoides</i>	80	Spawned as eggs	Lebour, 1937
<i>Nodilittorina cincta</i>	80	Spawned as eggs	Pilkington, 1971
<i>Nodilittorina unifasciata antipoda</i>	80	Spawned as eggs	Pilkington, 1971
<i>Echinella trochiformis</i>	90	Spawned as eggs	Lebour, 1945
<i>Littorinopsis scabra</i>	100	Eggs retained in mantle cavity, spawned as veligers	Struhsaker, 1966
<i>Littorinopsis melanostoma</i>	120 - 140	Spawned as eggs	Berry and Chew, 1973
<i>Littorina littorea</i>	130 - 170	Spawned as eggs	Linke, 1933; Fretter and Graham, 1962
<i>Bembicium nanum</i>	200 - 210	Veligers hatch from benthic egg mass	Anderson, 1961
<i>Bembicium auratum</i>	230 - 265	Veligers hatch from benthic egg mass	Anderson, 1962
Non-pelagic development to crawling juvenile:			
<i>Littorina saxatilis</i>	485	Ovoviviparous	Fretter and Graham, 1962
<i>Laevilittorina caliginosa</i>	500 ± 60 SD	In egg mass	This paper
<i>Macquarieella hamiltoni</i>	540 ± 120 SD	In egg mass	This paper
<i>Littorina littoralis</i> (= obtusata)	600	In egg mass	Fretter and Graham, 1962
<i>Laevilittorina coriacea</i>	600	In egg mass	Picken, 1979
<i>Laevilacunaria bennetti</i>	700 - 800	In egg mass	Picken, 1979
<i>Laevilacunaria antarctica</i>	800 - 1,000	In egg mass	Picken, 1979
<i>Pellilittorina peltita</i>	1,500 - 1,750	In egg mass	Picken, 1979
<i>Pellilittorina setosa</i>	1,500 - 1,750	In egg mass	Picken, 1979

□ Nomenclature changes for some species are according to Rosewater (1970) and Bandel and Kadolsky (1982).

* Egg diameter across egg membrane.

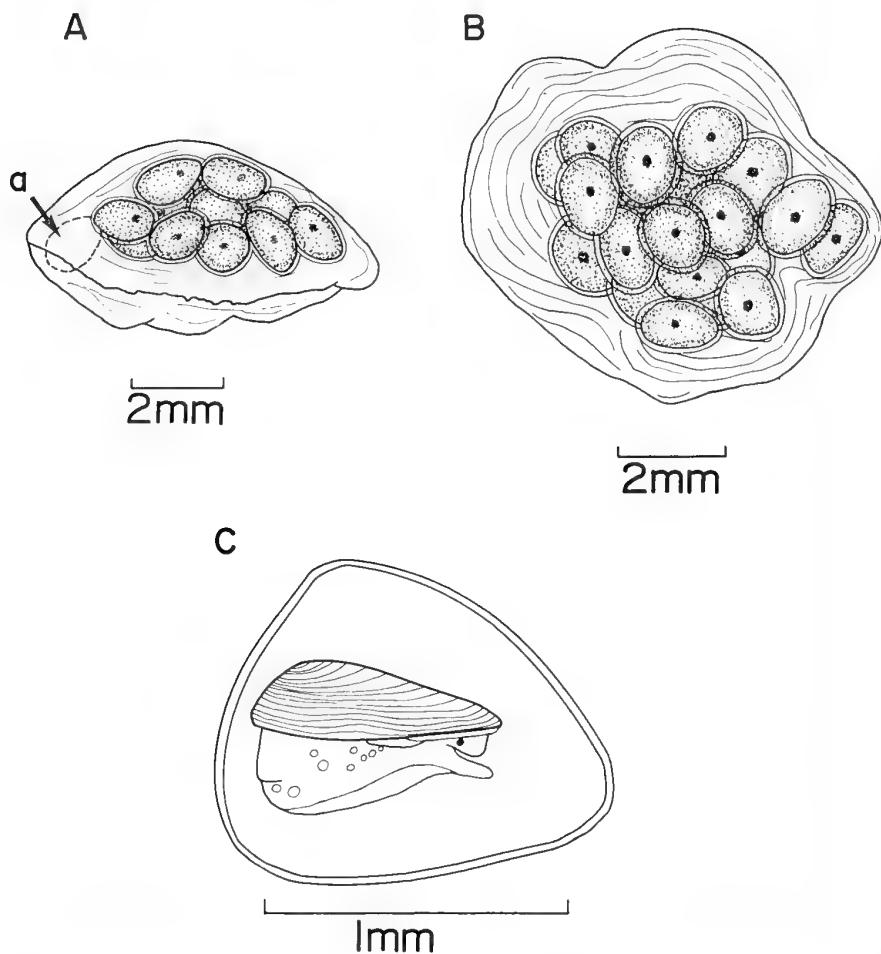


Fig. 1. *Kerguelenella lateralis* : A — lateral view of egg mass (a = empty egg compartment); B — dorsal view of egg mass; C — late stage embryo, prior to hatching.

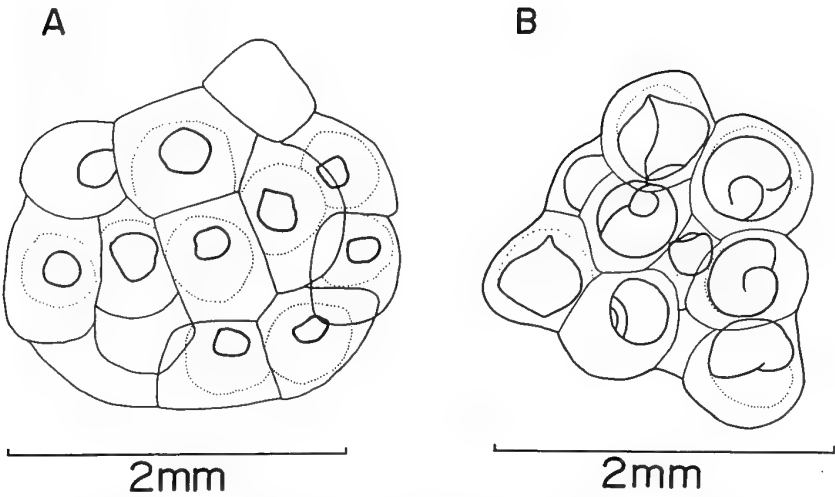


Fig. 2. *Laevilitorina caliginosa* : dorsal views of egg masses with early stage embryos (A) and late stage embryos (B).

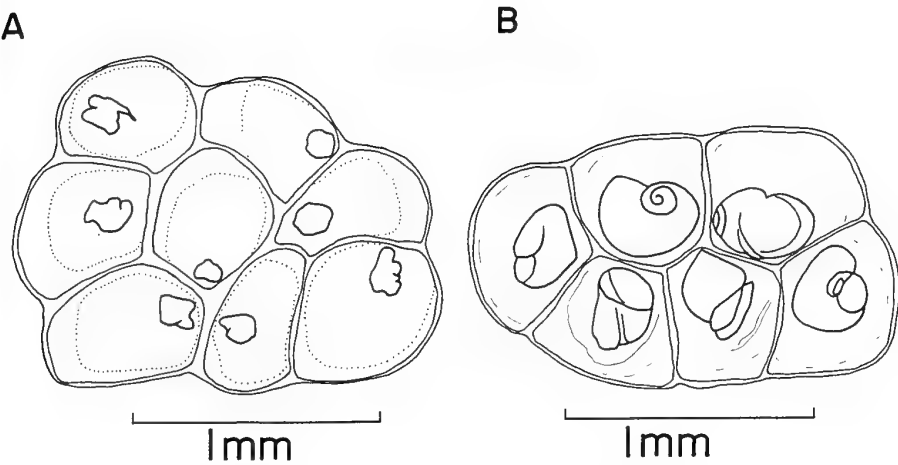


Fig. 3. *Macquariella hamiltoni* : dorsal views of egg masses with early stage embryos (A) and late stage embryos (B).

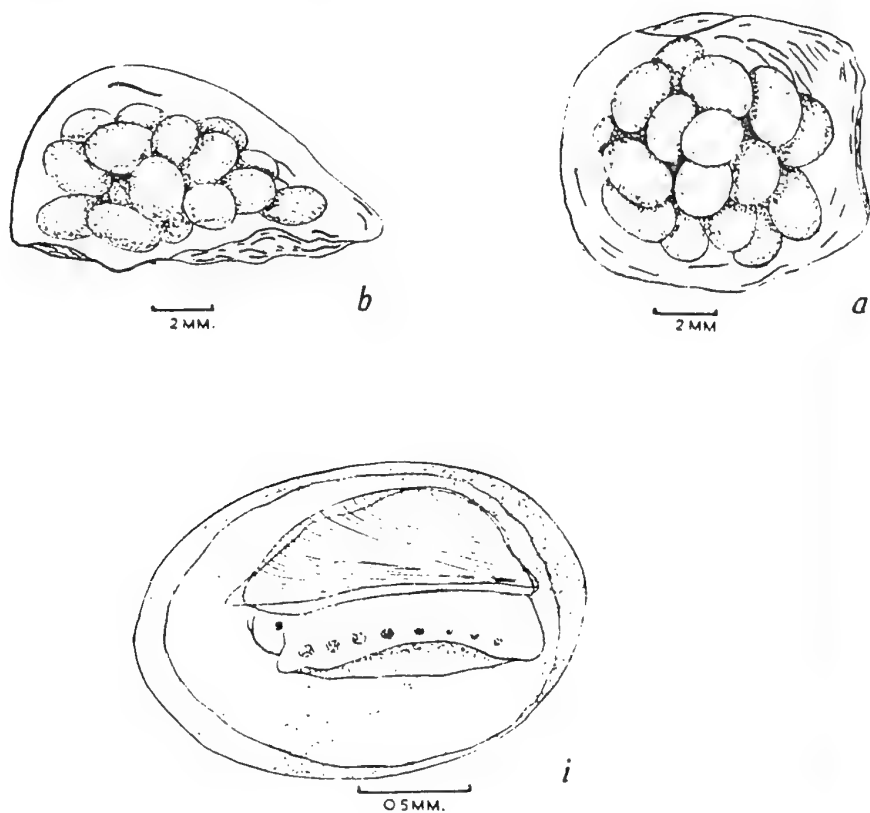


Fig. 4. Egg masses and late stage embryo of *Kerguelenella stewartiana*: b — lateral view of egg mass; a — dorsal view of egg mass; i — fully developed larva ready to emerge. From Knox (1955).

The taxonomic status of the opisthobranch mollusc *Bulla tenuissima* Sowerby 1868

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ABSTRACT

Based on an examination of type material, *Bulla tenuissima* Sowerby, 1868, described from Western Australia, is shown to be a synonym of *B. quoyii* Gray, 1843 of southern Australia and New Zealand. The range of the species in Western Australia is shown to be from the South Australian border to Carnarvon.

INTRODUCTION

Two species of the opisthobranch genus *Bulla* have been recorded from southwestern Australia: *B. quoyii* Gray, 1843 and *B. tenuissima* Sowerby, 1868. *B. quoyii* has been reported from various localities by several authors: Quoy and Gaimard (1833) (King George Sound and Princess Royal Harbour; as *Bulla australis* Quoy and Gaimard, 1833); Verco (1912) (Geraldton; as *Bulla australis* Gray, 1825); Hedley (1916) (based on the previous two records; as *Bullaria australis* (Gray, 1825); Hodgkin and Marsh (1957) (Perth area; as *Quibulla botanica* (Hedley, 1918) Macpherson and Gabriel (1962; as *Bullaria botanica* (Hedley, 1918); Hodgkin *et al.* (1966) (NSW to Houtman Abrolhos, WA; as *Bullaria botanica* (Hedley, 1918); and Roberts and Wells (1980) (Albany; as *Bulla quoyii* Gray in Dieffenbach, 1843). In an analysis of three species of *Bulla*, Willan (1978) recognised all of the above names as synonyms of *Bulla quoyii* Gray, 1843. *Bulla tenuissima* has also been recorded in Western Australia on several occasions: Sowerby (1868) (Swan River; type locality); Hedley (1916) (based on the Sowerby record); Macpherson (1954) (Recherche Archipelago); Hodgkin and Marsh (1957) (Perth area); and Chalmer *et al.* (1976) (Swan River) and in South Australia (Cotton and Godfrey, 1933). *Bulla quoyii*, (as *B. botanica*) has also been recorded in the W.A. fossil record by Reath (1925), Kendrick (1960) (both Swan River area) and Ludbrook (1978) (Roe Plains). Ludbrook (1978) considered the fossil history of the species to be from the Early Pleistocene to the Holocene.

There has been confusion in the separation of *B. quoyii* and *B. tenuissima*. Cotton and Godfrey (1933) regarded them as separate species but later (1938) believed them to be synonymous. Cotton (1959) regarded *B. quoyii* (as *Bullaria australis*), (Gray, 1825) as a synonym of *B. tenuissima*. However, Hodgkin and Marsh (1957) regarded the two as separate species. *B. tenuissima* was described as "2.5 cm, shell mottled light and dark brown, smooth, polished, thin. Animal light brown." The

habitat was listed as estuarine sandy bottoms. Only one figure was given which was intended to separate the two *Bulla* species from other gastropods. Macpherson and Gabriel (1962) recognised *B. quoyii* (as *Bullaria botanica*) as a valid species separable from *B. tenuissima*: "a small very thin-shelled species from Swan River, Western Australia." In his analysis of *B. quoyii*, Willan (1978) did not consider the status of *B. tenuissima*. The purpose of the present paper is to demonstrate that *B. tenuissima* is a synonym of *B. quoyii* and to clarify the range of the species in Western Australia.

TAXONOMY

1843. *Bulla quoyii* Gray, J.E. Catalogue of the species of Mollusca and their shells, which have hitherto been recorded as found at New Zealand, with the description of some lately discovered species. In Dieffenbach, E., Trav. N.Z. 2:243. Figures 1-3. Type locality: New Zealand.

1868. *Bulla tenuissima*, Sowerby, G.B. Conch. Icon. 16 (*Bulla*): plate 2, figure 4. Type locality: Swan River, W.A.

A comprehensive list of other synonyms is given by Willan (1978).

Type material examined:

Bulla quoyii — 10 syntypes from the British Museum (Natural History), registration numbers 1842.11.18.135-142.

Bulla tenuissima — 1 syntype from the British Museum (Natural History), registration number 197650.

Description of shell:

Shell thin, ovoid, with moderately convex whorls, up to 60 mm long (Figs. 1-2). The spire is depressed and surrounded by later whorls. The posterior lip margin is rounded, the outer lip is straight and the anterior margin is rounded. The aperture is white with the external colouration showing through. There is a pronounced white callus on the umbilical region which extends posteriorly along the inner margin of the whorl. The posterior aperture is narrow but it is greatly expanded anteriorly. The outer shell is smooth except for fine growth lines. A series of very fine spiral lines goes across the anterior base of the shell. These lines begin near the umbilicus but do not reach the outer lip. The shell is mottled with purple, grey, off-white and brown, often forming a zig zag pattern. The periostracum is light brown, but is absent in dead collected shells.

Discussion:

The original descriptions of *B. quoyii* and *B. tenuissima* were based only on dead shells. Rudman (1970; 1971) has provided some anatomical information on *B. quoyii*. Willan (1978) has shown that the shell of *B. quoyii* is variable in colour and shape. The Australian form reaches a larger size and had been thought to be lacking the fine spiral lines found in the New Zealand form. However on close examination, the Australian shells can be seen to have the spiral lines anteriorly. The type series of *B. quoyii* consists of ten syntypes ranging in length from 10.0 to 23.8 mm; the largest is an adult and the remainder are juveniles. The juvenile shells are fragile and have a much more rounded appearance than the adult (Figs. 3-6). The internal callus of the juveniles is faint. The syntype of *B. tenuissima* (Fig. 7), a juvenile 21.7 mm long, also has a faint callus and a fragile shell. In comparison with the *B. quoyii* type series, the *B. tenuissima* syntype is relatively longer and thinner. However this shell fits within the variation shown by Willan (1978) for *B. quoyii*, so *B. tenuissima* must be considered to be a synonym of *B. quoyii*.

Habitat:

On subtidal sand and seagrass beds to a depth of 41 m. Juveniles are also common in sand patches on platform reefs in the Perth area and at Rottnest Island. The species is nocturnal, emerging from the sand at night. It is frequently found on jetty pilings at night.

Range:

B. quoyii is a wide-ranging Australasian species. It occurs throughout the North Island of New Zealand and also extends into warmer bays in N.W. Nelson in the South Island. In Australia it extends throughout New South Wales, Victoria, Tasmania, and South Australia, and it reaches as far north as Carnarvon in Western Australia (present records). It is very rare in northern New South Wales and does not reach Queensland. Willan's (1978) record of Trinity Bay, Cairns, Qld. was erroneous (R.C. Willan, pers. comm. 1984). This range shows *B. quoyii* possesses a temperate distribution and not a tropically-based one as claimed by Roberts and Wells (1980).

W.A. Museum material from W.A.:

Recent: D and W are the number of dry and wet lots respectively): Eucla (1D); S. of Mundrabilla (1D); Duke of Orleans Bay (1D); 16 km east of Hopetoun (1D); Hamersley Inlet (1D); Bremer Bay (2D, 1W); Pallinup Estuary (1D); Cheyne Beach (1D); King George Sound (3D; 1W); Oyster Harbour (4D; 5W); Princess Royal Harbour (2D); Nornalup Inlet (1D); Windy Harbour, Pt D'Entrecasteaux (1D); Augusta (3D; 1W); Hamelin Bay (1W); Margaret River (1D; 1W); Kilcarnup (1W); Cowaramup Bay (4D); Cape Naturaliste (3D); Bunbury (2D); beach south of estuary, Mandurah (1D); Warnbro Sound (2D); Pt Peron (2D); Careening Bay, Garden I. (6D); other Garden I. (2D); west of Garden I. (2D; 1W); Cockburn Sound (6D; 5W); Carnac I. (2D; 1W); Stragglers Rocks (1D); off Fremantle (6D); Swan Estuary (7D; 1W); Leighton Beach (1D); Cottesloe (3D; 2W); Rottnest I. (1D; 3W); City Beach (1D); Triggs (3D); Yanchep (1D); Long I., Jurien Bay (1D); Green Head (2D); Greenough River (1D; 1W); Pelsart Group, Houtman Abrolhos (2D); Zeewyk Channel (1D); Easter Group (1D); Wallabi Group (8D); North I., Houtman Abrolhos (1D); Kalbarri (1D); Shark Bay (1D); Carnarvon (1W).

Fossil:

Roe Plains (12 lots); Madura (1); Esperance (1); Hamersley Inlet (1); Bremer Bay (5); Albany (2); Augusta (1); Vasse (5); Ludlow state forest (1); Leschenault Inlet (1); Capel (1); Myalup (5); Pinjarra (1); Mandurah (1); Rockingham (3); Kwinana (1); Thompsons Lake, Success (1); Fremantle (2); Attadale (1); Jandakot (7); Rottnest I. (5); Swan estuary (3); Peppermint Grove (14); Mosman Park (5); Cottesloe (1); Scarborough (1); Ocean Reef (1); Geraldton (3).

ACKNOWLEDGEMENTS

The loan of types was kindly arranged by K. Way of the British Museum (Natural History). C. Bryce took the photographs and G.W. Kendrick arranged access to the W.A. Museum fossil material and provided relevant information. R. Burn and Dr R. Willan kindly commented on a draft of the manuscript.

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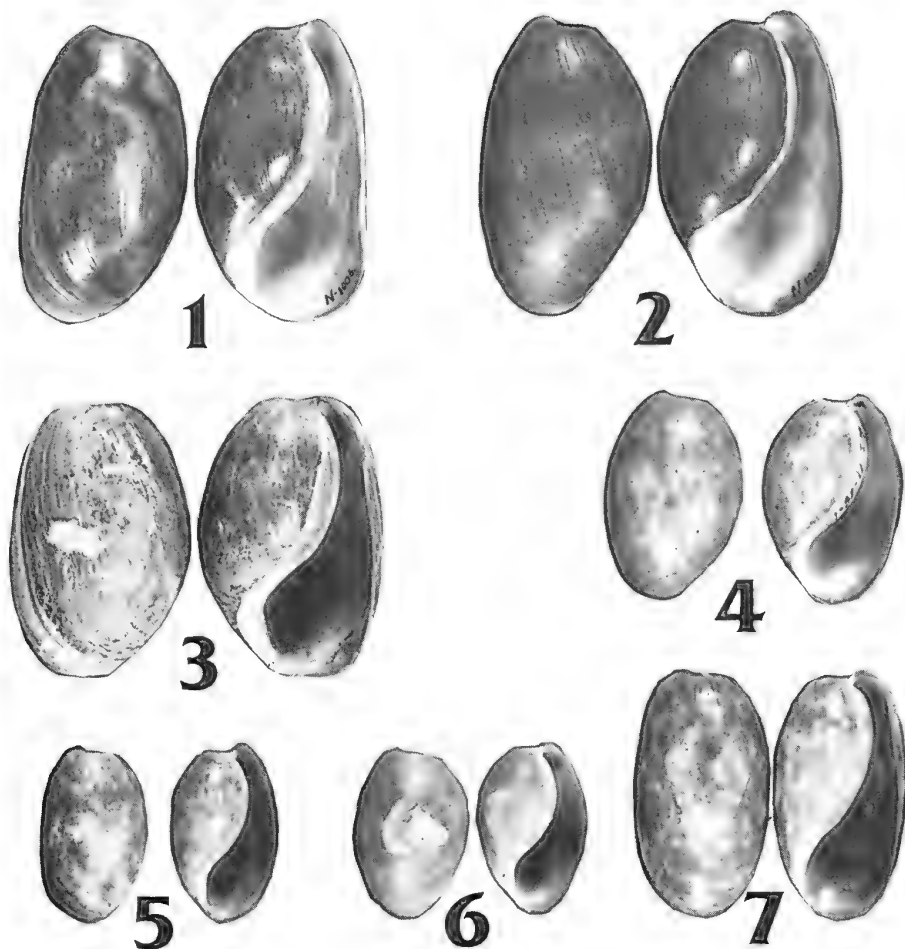


Plate 1. Figs 1 and 2. Adult specimens of *Bulla quoyii* from Emu Point, Albany, W.A. (WAM N.1000 (50.3 mm) and N.1003 (52.3 mm)). Fig. 3. Adult syntype of *B. quoyii* (BM(NH)) 1842.18.135). (23.8 mm). Figs. 4-6 Juvenile syntypes of *B. quoyii* (BM(NH) 1842.18.136-138), 17.4 mm, 15.3 mm and 14.8 mm in length. Fig. 7. Syntype of *B. tenuissima* (BM(NH) 197650) (21.7 mm).

Distribution and feeding of archaeogastropods in a boulder habitat at West Island, South Australia

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ABSTRACT

The vertical distribution and feeding of eleven species of archaeogastropod were examined on a boulder slope at West Island, South Australia. Most species occur throughout the depth range, but species which feed on drift seagrass and algae occur in higher density at about 4m depth.

All species are herbivorous and feed variously on geniculate and crustose coralline algae, *Petroderma* crusts, macrophytes and drift seagrass and algae. There are minor differences between the species in microhabitat and type of food eaten.

Removal experiments show that, in the short term, these archaeogastropods (together with chitons) control the growth of filamentous algae on the upper sides of boulders.

INTRODUCTION

Subtidal boulders contain a complex community of erect and crustose algae, crustose animals and mobile grazing and predatory animals. Herbivorous molluscs in particular, play an important role in regulating benthic algal structure by controlling algal growth (Luckens 1974, Lubchenko 1978, Rafaelli 1979, Brawley and Adey 1981, Underwood and Jernakoff 1981). In order to elucidate the mechanisms controlling such a complex system it is necessary first to identify functionally similar groups of organisms and then to discover their effect by manipulations. This paper primarily addresses the former of these objects. It describes the distribution and feeding of some archaeogastropod molluscs in a subtidal boulder community, at West Island, South Australia and adds to an accumulating corpus of information on its biology, e.g. the algal communities (Shepherd and Womersley 1970), grazing by a chiton guild (Kangas and Shepherd 1984), and ecology of abalone (Shepherd 1973, Shepherd and Turner in prep.).

MATERIALS AND METHODS

The north shore of Abalone Cove, West Island, (35° 36' 25" South; 138° 35' 27" East) is a boulder slope with boulders, mostly 30 - 40 cm x 20 - 30 cm, and 20 cm high from about 0.5m depth to 5m at low water. At six depth intervals, 0.5m and from 1 to 5m at 1m depth intervals, 10 boulders were thoroughly examined, and the archaeogastropods (excluding limpets) on both the boulder upper and under surfaces, and on rocks below the boulder, identified and counted. This survey was conducted in March 1983 and again in September 1983. In order to estimate the density of archaeogastropods, the area of each boulder was taken to be its projection on the horizontal plane.

Archaeogastropods were collected between May and September 1983, and preserved in 10% formal sea-water. The stomach contents of samples of each species were extracted and spread out on a slide or petri dish for microscopic examination. The contents were scanned along several parallel lines, and the material under the cross of the eyepiece at equidistant points identified to morphological group.

Plant material was categorised as coralline algae (geniculate and encrusting), *Petroderma* crusts*, filamentous algae, brown, red or green macroalgae, and seagrasses, in accordance with the functional group approach of Steneck and Watling (1982).

A night dive was made on 21/6/83, and the presence or absence of normally cryptic species on the upper surfaces of boulders noted.

Percentage similarity (Bray and Curtis 1957) between the diets of 11 species was calculated and a dendrogram grouping species by the nearest neighbour method (Field and McFarlane 1968) was used to discover associations in terms of diet between species.

In a short term manipulation four experimental structures were set up on sandy bottom adjoining the subtidal boulder slope on 19 September 1983. Each structure consisted of a concrete base and 10 - 15 boulders all contained within a metal frame. The boulders were covered with crustose corallines and *Petroderma* sp., but all grazing animals (archaeogastropods and chitons) were removed from them. The controls were boulders which remained undisturbed at the base of the boulder slope and were subject to grazing by gastropods and chitons. We did not specifically control for disturbance of boulders because other experiments concurrently in progress showed that similar structures of boulders but with grazing molluscs on them, remained in the same condition in terms of algal cover as natural boulders.

The growth of erect algae on boulders was sampled by carefully taking the boulder from the water and scraping off the algae and trapped sediment on the upper surface from an area of 25cm², with four replicates on different boulders. Algae were dried at 50°C for 24 hours to give dry weight biomass.

RESULTS

The distribution of macro-algal communities described by dominance criteria, on the boulder slope in Abalone Cove is given in Fig. 1. Above and below boulders crustose red and brown algae, encrusting sponge, bryozoans, and ascidians (see Kangas and Shepherd (1984) for detailed distributional data) are abundant throughout the depth range.

Seventeen species of archaeogastropods (excluding limpets and abalone) were recorded on the boulder slope. Information on depth range, mean density, size range, and number of gut contents of species analysed are given in Table 1; six of the species were too rare to allow a study of their feeding. The depth distribution and density (averaged for the two surveys) of the 11 commoner species above and below boulders are given in Fig. 2.

Only three of the species (see Fig 2) occur on the upper, as well as under, surfaces of boulders during daylight hours. No additional species were recorded on the upper surfaces of boulders during the single night dive.

* refers to non-calcified algal crusts mostly of the genus *Petroderma*.

Two species showed substantial differences in abundance between the March and September censuses (Fig. 3). The *G. preissiana* population was mainly juveniles in September and adults in March, implying a recruitment at 4–5 m depth and later upward migration. *D. odontis* tends to occur in clusters and the differences in Fig. 3 may be a sampling artifact.

The proportional abundance of different food types in the gut of 11 species is shown in Fig. 4. All species are herbivorous, with several food types commonly present in the gut. In some species small amounts of animal matter (mostly sponge but forams in the case of *P. ventricosa* and *G. imbricata*) are present in the gut, and are probably taken incidentally.

The dendrogram (Fig. 5) showing dietary similarities between species discloses several species groupings, some of which coincide with microhabitat differences between species. In general there is high overlap in diet between groups.

The first group, *G. preissiana*, *C. plebejus* and *E. aspersus* shares the same microhabitat on the underside of boulders and feeds mainly on sea-grass and crustose coralline algae. Extensive *Posidonia* beds and occasional patches of *Heterozostera tasmanica* occur on adjoining sandy bottom, and drift blades of these seagrasses and algae are abundant under and between boulders.

These species feed on drift, but not living, seagrasses. Except for *G. preissiana*, which eats considerable amounts of *Zonaria* spp. (27%), they eat little macroalgae.

The second group *T. undulatus*, *T. torquatus* and *P. ventricosa* live on the upper sides of boulders (except small *P. ventricosa*) and graze mostly on macrophytes and geniculate coralline algae (mostly *Haliptilon* spp.) The macrophytes eaten differ according to species. *T. undulatus* feeds on *Ecklonia*, (28%) on whose fronds it is commonly found, and green algae of the genus *Caulerpa* (27%). The other species take mostly brown algae of the genera *Cystophora* (sporelings and juveniles), *Halopteris*, *Dictyota*, *Pachydictyon* and *Lobospora*. The last two genera are common in the drift (Shepherd 1973) and are probably taken as detritus.

The species of the third group, *D. odontis* and *B. squamifera*, occur on the upper sides of boulders and feed substantially on crustose corallines and the same genera of brown macroalgae listed for the previous group.

Of the fourth group, *C. limbatus* lives on the under sides of boulders and *G. imbricata* in sand or gravel under boulders. Both species graze on crustose and geniculate corallines as well as taking drift seagrass and some brown macroalgae.

The last species *S. antipodes* lives on the under sides of boulders or in fissures, where it feeds exclusively on drift macroalgae and seagrass, as do the abalone *Haliotis scalaris* and *H. laevigata* in the same habitat (Shepherd 1973).

Experimental Removal of Archaeogastropods

By 23 November 1983, after 65 days, a low turf of erect, filamentous algae to about 5 mm high, mostly *Polysiphonia sertularioides* had grown on the upper surfaces of the boulders in the four structures kept free of grazing molluscs. Mean biomass (d.w.) of the turf algae was 19 mg cm⁻² (s.e. 4 mg) and of the trapped sediment 87 mg cm⁻² (s.e. 4 mg). On boulders subject to natural grazing there was no algal turf and little sediment (3.7 mg cm⁻², s.e. 0.6 mg). On the same date three of the turf-covered boulders from the structures were replaced among other boulders at the base of the boulder slope. When inspected on the following day a number of *D. odontis* and *B. squamifera* and their grazing trail marks were observed on the turf. By 30 November 1983 the algal turf was gone exposing the crustose layer of apparently dead crustose corallines. Ungrazed boulders in the structures were still covered by filamentous algae and sediment, and the original grazed control boulders still retained a healthy layer of crustose algae. It was concluded that in the absence of grazing molluscs filamentous algae covered upper surfaces of boulders and, with entrapped sediment, smothered the crustose algal layer.

DISCUSSION

Guilds of grazing archaeogastropods have received little attention in the literature and this is the first such study for southern Australian waters. The diversity of species matches that of chitons at the same site (Kangas and Shepherd 1984) and they are similarly distributed throughout the depth range. In contrast with the chitons, however, these archaeogastropods appear to prefer a habitat free of sediment and so decline in abundance at 5m depth, where rock is buried by sand. However, the abundance of drift seagrass, epiphytes and drift macroalgae at 4 - 5m depth may account for the increased abundance at about 4m deep of those species (*M. plebejus*, *P. ventricosa* and *S. antipodes*) which feed on them.

Hawkins and Hartnoll (1983) considered that most archaeogastropods are generalist grazers feeding on whatever is available. However, Steneck and Watling (1982) suggested that the rhipidoglossan radula of archaeogastropods, with its lack of buccal strength and inherent weaknesses in tooth structure was ill-adapted to rasping leathery macrophytes or coralline algae. While the species considered in this paper have a much more varied diet than predicted by Steneck and Watling's scheme, the minor differences between their diets suggest some choice of food. Given the need for caution in inferring food preferences from gut contents, the abundance of macroalgae, corallines, crustose species and algal drift in the habitat imply that consistent differences are likely to be real ones, particularly if they coincide with micro-habitat differences between species. However, filamentous algal species, rare in the boulder habitat, may be preferred by several of the grazers, as demonstrated by the rapidity with which they were grazed from the ungraded boulders replaced on the boulder slope.

The removal experiment suggests that archaeogastropods and chitons together control the growth of filamentous algae on the rock surface. The chitons *Chiton diaphorus* and *Chiton calliozonus* (Kangas and Shepherd 1984) and the archaeogastropods *D. odontis* and *B. squamifera* observed in this study all graze on the upper surfaces of boulders and appear to be the principal agents of such control. Sediment and algal films are known to inhibit the growth of crustose algae (Slocum 1980 and review of Hatcher 1983) and the decline of crustose corallines and *Petroderma* on ungrazed boulders is consistent with this. Thus grazing by these archaeogastropods might be expected to influence considerably the algal community structure. This can best be shown by longer term experiments.

This study and that of Kangas and Shepherd (1984) show that at least 22 species of archaeogastropods and chitons share the same boulder habitat and have strongly overlapping diets. How is this co-existence maintained? It is possible that they have partitioned their resources in subtle ways and are in stable co-existence without serious inter-specific competition (Kohn 1959, Ayal and Safriel 1982). Alternatively they may be able to tolerate a high similarity in requirements without their co-existence becoming precarious (MacArthur 1972). Another possibility, that is more easily testable, is that predators prevent the molluscan populations increasing to a level where competition for resources may occur. Studies on the effect of predation by wrasses, which are abundant in the area, and known to feed on these molluscs would be valuable.

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Table 1 Species of grazing gastropods on the boulder slope at West Island, with depth range, mean density, mean size and size range, and number of gut contents analysed. In each case the length measurement is columellar length.

Species	Depth (m)	Mean Density (Nos. m ⁻²)	Length (mm)	Number Used in Feeding Study
<i>Scutus antipodes</i> (Montfort)	4-5	2.9	38-90	8
<i>Clanculus (Eurclanculus) limbatus</i> (Quoy and Gaimard)	1-5	10.2	13-21	10
<i>Clanculus (Mesoclanculus) plebejus</i> (Philippi)	0.5-5	44.6	6-8	10
<i>Diloma (Chlorodiloma) odontis</i> (Wood)	0.5-5	5.5	16-22	10
<i>Gibbula (Notogibbula) preissiana</i> (Philippi)	1-5	12.7	7-8	10
<i>Granata imbricata</i> (Lamarck)	1-5	6.2	24-35	10
<i>Euchelus aspersus</i> (Philippi)	1-4	2.3	7-10	10
<i>Turbo (Subnina) undulatus</i> (Solander)	0.5-5	9.8	26-40	10
<i>Turbo (Ninella) torquatus</i> (Gmelin)	1-4	1.1	28-74	8
<i>Bellastraea squamifera</i> (Koch)	3-5	5.7	13-15	10
<i>Phasianella ventricosa</i> (Swainson)	2-5	12.9	8-14	10
Rare species not used in feeding study				
<i>Cantharus (Phasianotrochus) eximius</i> (Perry)	3	<0.1	18-25	-
<i>Thalotia (Prothalotia) lehmanni</i> (Menke)	3-5	<0.1	16-20	-
<i>Thalotia (Prothalotia) pulcherrima</i> (Wood)	3-5	<0.1	13-18	-
<i>Clanculus (Macroclanculus) undatus</i> (Lamarck)	1-4	<0.1	24-30	-
<i>Clanculus (Mesoclanculus) consobrinus</i> (Tate)	2-5	<0.1	14-15	-
<i>Stomatella auricula</i> (Lamarck)	4-5	<0.1	10-14	-
			Mean	
			61.1	
			19.1	
			7.3	
			18.8	
			7.8	
			28.2	
			8.7	
			33.8	
			43.0	
			14.3	
			28.2	
			21.5	
			18.0	
			15.5	
			27.0	
			14.5	
			12.0	

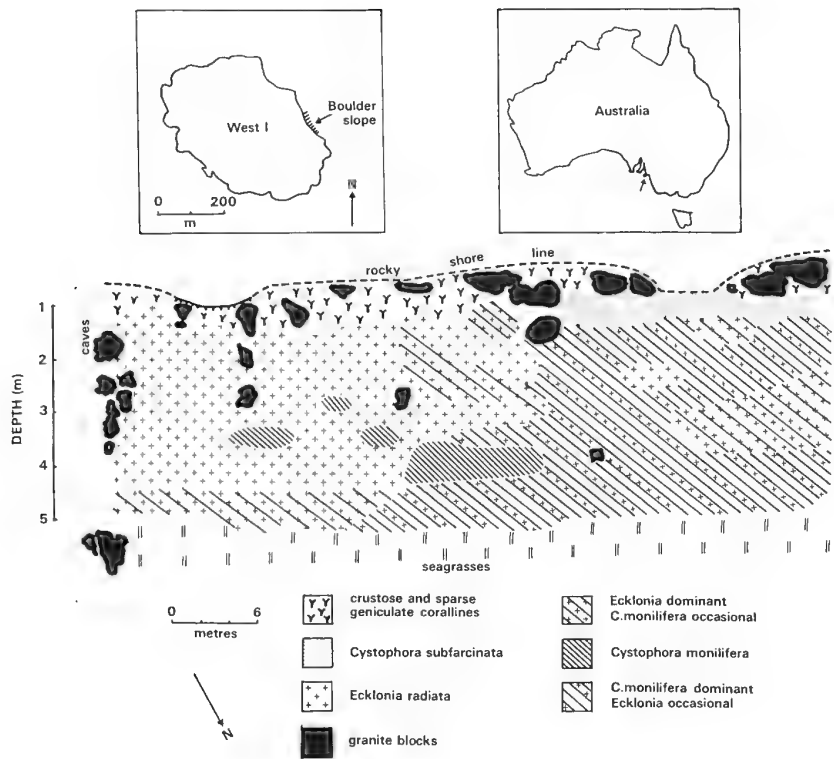


Fig 1. Map of West I. showing the algal communities of the boulder slope in Abalone Cove. The granite blocks shown are prominent topographic features bearing similar algal communities to surrounding boulders.

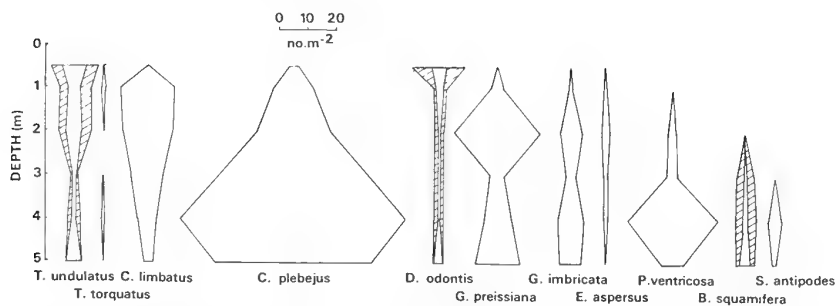


Fig 2. Distribution with depth of density of archaeogastropods on the upper (hatched) and lower (blank) sides of boulders.

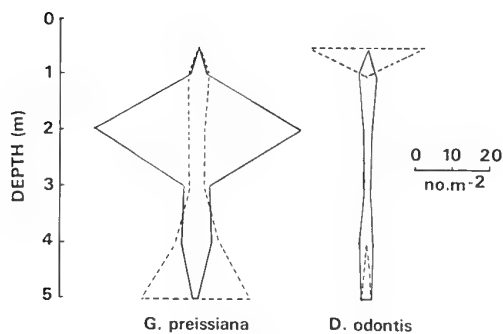


Fig 3. Distribution with depth of density of *G. preissiana* and *D. odontis* in March (continuous line) and September (dashed line) 1983.

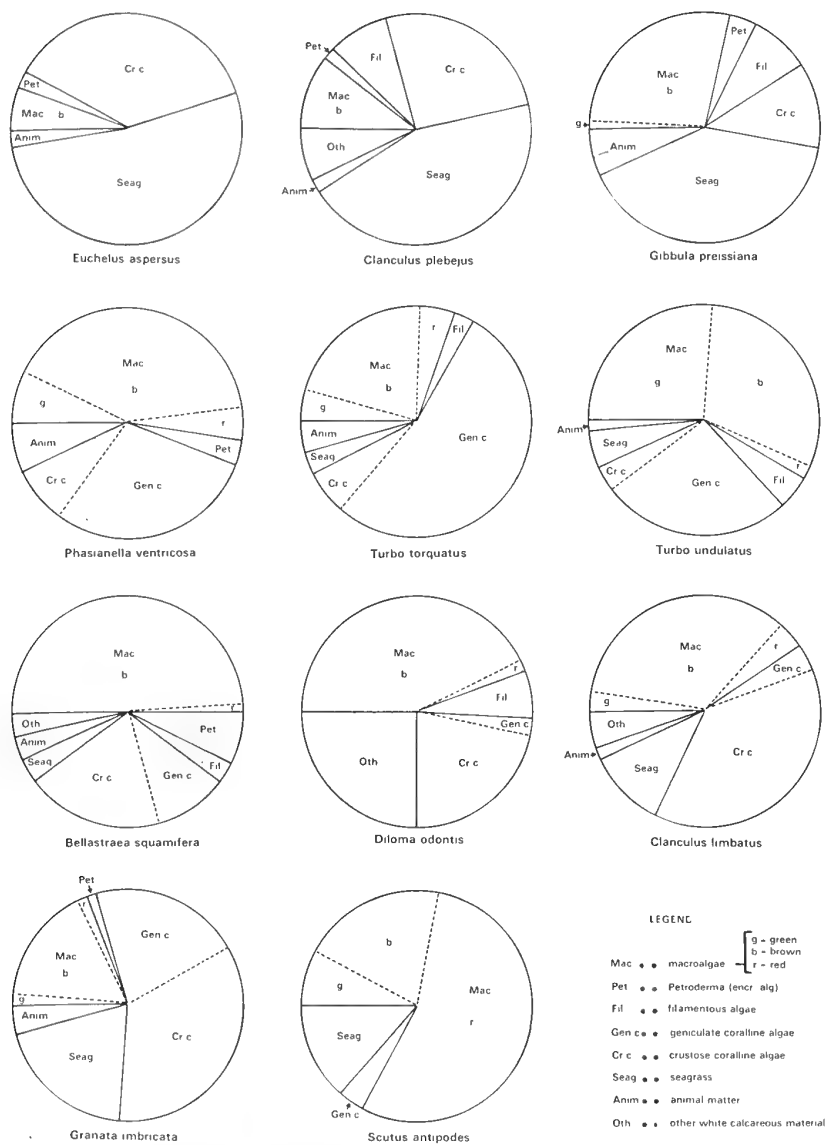


Fig 4. Mean percentage composition of food categories in the gut of 11 species of archaeogastropod grouped according to affinities in diet (see Fig. 5).

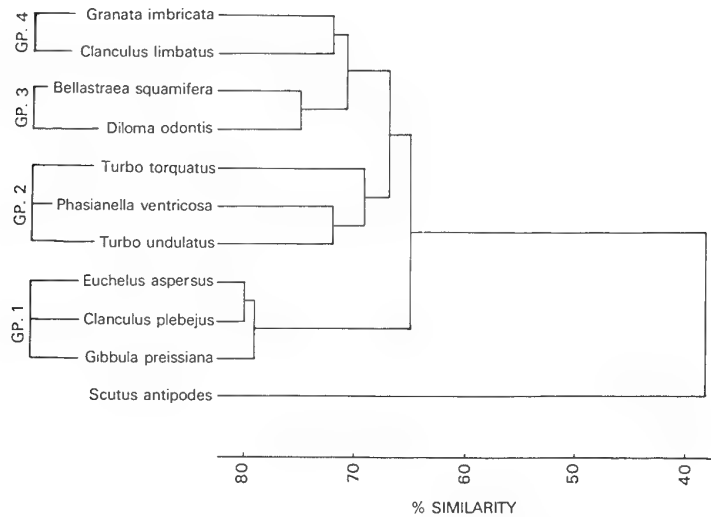


Fig 5. Dendrogram showing affinities in diet between 11 species of archaeogastropod.

The genus *Dermomurex* (Mollusca:Gastropoda) in Australia

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ABSTRACT

The muricid genus *Dermomurex* has been thought to include only three species in Australia: two of Miocene age and one Recent form. But examination of museum collections has revealed an additional seven species are referable to this genus. The genus as revised now includes:

Dermomurex s.s. Miocene-Recent: *D. garrardi* sp. nov., *D. goldsteini* (Tenison-Woods), *D. angustus* (Verco);

Dermomurex (*Takia*) Oligocene-Recent: *D. (T.) imitator* sp. nov., *D. (T.) cretaceus* sp. nov.; *D. (T.) glebosus* sp. nov., *D. (T.) pachystirus* (Tate);

Dermomurex (*Viator*) Miocene-Recent: *D. (V.) darraghi* sp. nov., *D. (V.) asteriscus* (Tate), *D. (V.) antonius* Vokes.

INTRODUCTION

Knowledge of the presence of the genus *Dermomurex* in Australia, both in the Recent fauna and in the fossil record, has been concealed from the world by a series of misidentifications and general lack of interest in the fossil fauna since the time of Tate (1888). In 1971, when the writer compiled a taxonomic catalogue of the genus *Murex* Linné (i.e., all species that originally had been named as "*Murex*"), she included only three Australian species of this group: "*M.*" *asteriscus* Tate, 1888, and "*M.*" *pachystirus* Tate, 1888, which were assigned to *Dermomurex* (*Takia*), and "*M.*" *crassiliratus* Tate, 1888, assigned to (?)*Dermomurex* s.s.

In a subsequent paper (Vokes, 1974a), a Recent species from the Dampier Archipelago was named as type of a new subgenus: *Dermomurex* (*Viator*) *antonius*; and the species "*M.*" *asteriscus* was transferred to this new subgenus. It was suggested (Vokes, 1974b, p. 8) that the American *D. sexangulus* (Dall, 1915) was a possible ancestor to the line, although this called for a great amount of "remarkability", as the species had to travel half-way around the world. But the alternative of having the Australian and American forms derived by parallelism was equally remarkable.

Then, in 1980, the writer had the pleasure of spending some time working at the Australian Museum and discovered that these species had several unrecognised companions, including three additional members of the subgenus *Takia*, three species of *Dermomurex* s.s., and one new *Viator*.

However, it was ascertained that "*M.* *crassiliratus*" is not a *Dermomurex*, as had been assumed previously on the basis of the original illustration. A photograph of the holotype (in the collections of the South Australian Museum) shows clearly that the shell is a *Pygmaepterys*, allied with the living *P. funafutiensis* (Hedley, 1899). Nevertheless, this leaves us with a total of ten species, where we formerly had but three, an impressive array by any standards.

To begin with the Recent fauna, there are two species that should be assigned to *Dermomurex* s.s.: "*Trophon*" *goldsteini* Tenison-Woods and "*Trophon*" *angustus* Verco. These two, originally named as *Trophon* have customarily been assigned to *Litozamia*, on the basis of Iredale's statement in his "description" of that genus: "The minute shore shells such as *rudolphi*, *goldsteini*, and *brazieri* may be named *Litozamia*" (Iredale, 1929, p. 185). But other than their small size and the presence of an intritacalx there is only a superficial resemblance between *goldsteini* and *angustus* (which is placed near *goldsteini* because of the valid comparison with that species in the original description) and the true *Litozamia* species: *rudolphi* (Brazier, 1894), which is the type; and *brazieri* (Tenison-Woods, 1876), the only other species to be referred to the genus. These two are more fusoid in outline and have only rounded varical ridges rather than true varices. The intritacalx, although relatively thick for a *Trophon*, is much thinner than that of a *Dermomurex*, and is neither tunneled nor deciduous. (This peculiar layer only recently recognised and named by D'Attilio and Radwin, 1971, is figured in an enlarged photograph in Vokes, 1974a, pl. 1, fig. 2.)

The intritacalx is perhaps the single most distinctive feature in the genus *Dermomurex*. Its presence was first noted in the living Australian species by Verco, who stated for "*T.*" *angustus*: "The shell has an inner hard enamel-like layer, and an outer of soft, porous, chalky consistence. This when perfect is nearly smooth, longitudinal and transverse markings being scarcely visible. When slightly denuded coarse and fine longitudinal lines become evident" (Verco, 1895a, p. 87). He further elaborated for "*T.*" *goldsteini*: "The shell in life is composed of two distinct layers, an inner enamel-like foundation and an outer sordid white, loose textured, soft chalk-like coating. In perfect specimens this is smooth, but when very slightly worn, it shows numerous spiral and longitudinal fibres or incisions" (Verco, 1895b, p. 97).

In spite of this excellent description, the species have never been recognised as *Dermomurex*, even by this writer. In partial explanation there may be offered only the fact that when a specimen of "*T.*" *goldsteini* was borrowed several years ago to examine this described intritacalx (which sounded very like a *Dermomurex*), the specimen received was found later to be *rudolphi*! The same shell was figured by Kaicher (1980, no. 2535) as "*Litozamia goldsteini*," on the basis of this erroneous identification, which is only one more example of the problems that have plagued the Australian species of *Dermomurex*. From the beginning it has been a comedy of errors, perpetuated principally by the fact that no adequate figure of either species has ever been published.

In addition to the two Recent members of *Dermomurex* s.s., there is a third fossil species in the collections of both the Australian Museum and the National Museum of Victoria, misidentified in the first case as "*Murex*" *bifrons* Tate, 1888, and in the second as "*Murex*" *didymus* Tate, 1888. Both of the latter are unquestionably valid members of the genus *Pterynotus* and actually bear little more than a family resemblance to this new form, here named *D. garrardi*. All specimens seen come from the famous Balcombian locality at Fossil Beach, near Mornington, Victoria.

In the subgenus *Viator*, as noted above, previously recognised are the Balcombian *D. asteriscus* (Tate) and the Recent *D. antonius* Vokes. In the collections of the National Museum of Victoria there are five examples of another new species that is closely allied with *D. asteriscus*, but is Longfordian-Batesfordian in age. It is here described as *D. darraghi*.

When the possibility of the American *D. sexangulus* being ancestral to the Australian *Viator* line was suggested by the writer (Vokes, 1974b), it was noted that the American species occurred in a peculiar locality, which seemed more allied to the European faunas than to the American. In the collections of the National Museum of Victoria the writer located a specimen from Bird Rock Cliff, near Torquay, Victoria, that was so nearly like *D. sexangulus*, as to appear at first glance the identical species. Closer examination revealed certain differences between the two and the Victoria shell is here named *D. imitator*.

The beds at Torquay have been referred to the Jan Juc Formation, for which the age has been cited variously as anywhere from Eocene to Miocene. Because of the presence of this species so nearly identical with one that occurs in the United States, a sample of the matrix from the aperture of the Australian shell was given to Dr W.H. Akers, micropaleontologist with the Chevron Research Laboratory, who advised that, on the basis of the foraminifer genus *Neorotalia*, the age was latest Oligocene or basal Miocene — which is exactly the same age (Chickasawhayan) as the beds at Silverdale, North Carolina, where *D. sexangulus* occurs. This is the same conclusion presented by Ludbrook (1973, p. 248-251), who has well summarised the nature of the conflicting data.

Thus, it would seem that we must go farther back in geologic time to find a common ancestor for the Australian and American species. Although there are good species of *Takia* in the early Oligocene of North America (*D. cookei* Vokes, 1975) and in the late Oligocene of France (*D. cotteavi* Meunier, 1880) neither of these is especially close to the morphotype exhibited by *D. sexangulus* and its Australian mimic, both of which are characterised by an inflated body whorl, a relatively low spire, very strong varices, and an expanded parietal lip much like the living *D. infrons* Vokes, 1974. Presumably, the ancestry of the line lies hidden somewhere in the Tethyan Eocene fauna of which the American and Australian forms represent the two extremes of distribution.

In addition to the aforementioned, in the Victorian collections there are many examples of another new species of early Oligocene age, which had been identified as the species cited in a list by Tate (1895) as *D. cretaceus*, a name the writer is happy to adopt. This new species is extremely common in the Glen Aire Formation at Cape Otway.

Although a member of the subgenus *Takia*, *D. cretaceus* does not seem to be in the general line of the development to the living representative of the group, *D. infrons* Vokes, type of the subgenus, but rather is a more elongate form and seems to be ancestral to yet another new species that occurs in the Pliocene Roe Calcarene of the Madura area in Western Australia, described herein as *D. glebosus*.

In summary, we now see in the Australian fauna, fossil and Recent, a total of ten species of **DERMOMUREX**, to wit:
Dermomurex s.s.

GARRADI Vokes, sp. nov. - Balcombian

goldsteini (Tenison-Woods, 1876) - Kalimnan - Recent

angustus (Verco, 1895) - Recent

Subgenus **Takia**

CRETACEOUS Vokes, sp. nov. — “Late Aldingan”

IMITATOR Vokes, sp. nov. — Jankjukian

pachystirus (Tate, 1888) — Batesfordian-Balcombian

GLEBOSUS Vokes, sp. nov. — Pliocene

Subgenus **Viator**

DARRAGHI Vokes, sp. nov. — Longfordian-Batesfordian

asteriscus (Tate, 1888) — Balcombian

antonius Vokes, 1974 — Recent

The remainder of the Indo-Pacific area has another five species: *Dermomurex* (s.s.) *quilonica* (Dey, 1962), from the middle Miocene of India; and *D. (Triatella) acuticostatus* (Wanner and Hahn, 1935) from the Miocene of Java; and the living forms: *D. (Triatella) neglecta* (Habe and Kosuge, 1971) from the Philippine Islands; *D. (Takia) infrons* Vokes, 1974, from southern Japan, and *D. (Takia) bobyini* (Kosuge, 1984), also from the Philippines.

In 1975 the writer noted that there were relatively few species of *Dermomurex* to be divided up among five subgenera — 32 at that writing. In the present work we have added seven and in another paper (Vokes, *in press*) on the fossil fauna (Mio-Pliocene) of the Dominican Republic (Caribbean) there are an additional four new species. It would seem that the scarcity of species is more a reflection of lack of knowledge than lack of taxa. Although the problem is most acute in the fossil faunas, especially in the Indo-Pacific area, it is still a factor in the living faunas. In 1976 the writer recognised *D. alabastrum* (Adams) as another Caribbean species; in 1978 she named *D. (Takia) africanus* from East Africa; in 1979 Petuch named *D. (Trialatella) oxum* from off the coast of Brazil; in 1984 Kosuge named *Takia bobyini* from the Philippines; and even in the extremely well known fauna of the Tropical East Pacific (Mexico to Ecuador) there is another new species *D. gunteri* (Vokes, 1985) just described. In less than ten years we have gone from 32 species to 48.

Dividing lines between the various subgenera of *Dermomurex* are not always well delineated and it has been suggested that perhaps all should be included in the single taxon *Dermomurex* s.s. as was done by Radwin and D'Attilio (1976, pp. 44-77), who only treated 9 species, however. But we should not lose sight of the fact that taxonomy is much like a rainbow. We are attempting to divide a continuous spectrum into discrete groups. There must invariably be intermediate forms.

In the genus *Dermomurex* species usually begin with six (rarely five, seven or eight) varices on the early post-nuclear whorls. In *Dermomurex* s.s. and *Trialatella* Berry, 1964, the number is gradually reduced to only three varices on the later whorls. In *Gracilimurex* Thiele, 1929, the number is reduced to two, mimicking the closely related genus *Aspella* Mörch, 1877. In *Takia* and *Viator* the original six varices persist into adulthood. But, in addition to the number of varices, there is also an overall difference in shell shape: *Dermomurex* s.s. and *Gracilimurex* have an elongate spire and a very short siphonal canal, so that the proportion of spire height to aperture is equal to or in excess of 50%. The other subgenera have low spires and elongated canals. *Trialatella* and *Takia* are similar in having moderately long canals but *Trialatella* has only three greatly expanded varices, in contrast to the persistent six of *Takia*. *Viator* differs from *Takia* in having a very elongate straight canal. One might suggest a comparison between *Murex* s.s. with its long straight canal and *Chicoreus* Montfort, 1810, which has a short, recurved canal.

As far as this writer is concerned, the elongation of the canal is of as much taxonomic relevance as the number of varices. Thus, the distinction between *Dermomurex* s.s. and *Takia* is as much the short vs. long canal as it is the three vs. six varices. (It is useful to compare the illustrations on plate 1 and 2.) Therefore, even though the Australian species *D. goldsteini* and *D. angustus* retain six varices, in overall shell shape they seem closer to *Dermomurex* s.s. than to *Takia*.

A simple key separating the subgenera of *Dermomurex* might be as follows:

I. Spire short

A. Six varices

1. moderate canal — *Takia*

2. long straight canal — *Viator*

B. Three varices — *Trialatella*

II. Spire elongate

A. Two varices — *Gracilimurex*

B. Three to six varices — *Dermomurex* s.s.

SYSTEMATIC DESCRIPTIONS

Family MURICIDAE da Costa, 1776

Subfamily MURICINAE da Costa, 1776

Genus DERMOMUREX Monterosato, 1890

Poweria MONTEROSATO, 1884, Nomen. Conch. Medit., p. 113. (*Non Poweria* Bonaparte, 1840).Type-species: *Murex scalarinus* Bivona-Bernardi, by original designation [*Murex scalarinus* Bivona-Bernardi, 1832, =*Murex scalaroides* Blainville, 1829].*Dermomurex* MONTEROSATO, 1890, Natural. Sicil., v. 9, p. 181. New name for *Poweria* Monterosato non Bonaparte.*Hexachorda* COSSMANN, 1903, Essais Paléoconch. Comp., v. 5, p. 47. Type-species: *Murex tenellus* Mayer, 1869, by original designation.

Subgenus DERMOMUREX s.s.

DERMOMUREX (DERMOMUREX) GARRARDI E.H. Vokes, sp. nov.

Plate 1, figs. 1-4

Description: Shell elongate-fusoid; protoconch of one and one-half smooth, polished whorls; teleoconch of six additional whorls. Spiral ornamentation beginning very faintly on approximately third post-nuclear whorl with slightly raised cords, four or five on the body whorl. Axial ornamentation on first post-nuclear whorl of six small varices that overlap onto the protoconch; continuing for about four or five whorls with six narrow ridge-like varices, then evanescent to only three on the penultimate and last whorls, that at the aperture always the largest. Aperture elongate-oval, with a thin parietal lip contiguous with the outer lip, both completely smooth. Siphonal canal moderately long, almost closed over by a narrow flange of shelly material; terminations of former canals melded in an essentially continuous curved line forming an umbilical chink. In life the exterior of the entire shell covered by a thick intritacalx, probably completely smooth, but in the fossil state always more or less eroded, showing strong spirally oriented tunnels crossed by finer axial growth lines(?), giving a reticulated appearance to the remaining material. The shell surface beneath the intritacalx almost totally smooth, marked only by faint spiral cords and varical ridges.

Holotype: National Museum of Victoria P 74477; height 16.0 mm, diameter 6.5 mm (Plate 1, fig. 1).

Paratype A: Australian Museum C.131237; height 13.4 mm, diameter 5.2 mm (Plate 1, fig. 2).

Paratype B: South Australian Museum P 23845; height 11.6 mm, diameter 5.0 mm (Plate 1, fig. 3).

Paratype C: Australian Museum C.121237a; height 11.0 mm, diameter 5.5 mm (Plate 1, fig. 4).

Other material studied: National Museum of Victoria P 74071 — 74073 [as *Litozamia didymus* (Tate, 1888)] collected by F.A. Cudmore; Australian Museum C.125237 [8 specimens, as *Pterynotus bifrons* (Tate, 1888)], collected by T.R. Garrard and J. Kerslake; locality of all same as type locality.

Type locality: Fyansford Formation (=Balcombe Clay; Balcombian), Fossil Beach, "2 miles" (3.7 km) south of Mornington, Victoria.

Discussion: This middle Miocene species has little relationship to any known living forms, with the possible exception of the Philippine *D. neglecta* (Habe and Kosuge, 1971). That species is lower spired with greatly expanded varical flanges and is assigned to the subgenus *Trialatella*; however, if we had an unworn example of *D. garrardi* it also might have these varical extensions, for the bulk of the varix is formed of intritacalx, not shelly material (compare pl. 1, fig. 7). This is one of the difficulties in attempting to relate fossil and living species of *Dermomurex*. This fragile layer is invariably lost in the fossil state and only remnant patches remain to suggest the former covering layer. Certainly the new species is not closely related to the living *D. goldsteini* and *D. angustus*, both of which retain six varices throughout their life-span. However, they do all share a non-denticulated aperture, which is unique to these Australian forms and *D. neglecta*.

This new species is not especially rare but is known only from the type locality. The majority of the specimens (8 of the 11), including all of the figured type material, was collected by T.R. Garrard and J. Kerslake of the Australian Museum; therefore, it is with pleasure that this new species is named in honour of Mr Tom Garrard, who has contributed so much to the collections at that Institution.

DERMOMUREX (DERMOMUREX) GOLDSTEINI (Tenison-Woods, 1876)

Plate 1, figs. 5, 6

Trophon goldsteini TENISON-WOODS, 1876, Proc. Roy. Soc. Tas. for 1875, p. 136.

Trophon goldsteini Tenison-Woods. VERCO, 1895, Trans. Roy. Soc. So. Aust., v. 19, p. 97, pl. 1, figs. 4, 4a, 5 (said to be fig. 4b).

Trophon goldsteini Tenison-Woods. MAY, 1923, Illus. Index Tasmanian Shells, pl. 40, fig. 1.

Litozamia goldsteini (Tenison-Woods). IREDALE, 1929, Rec. Aust. Mus., v. 17, p. 185.

Litozamia goldsteini (Tenison-Woods). COTTON, 1956, Publ. Roy. Soc. So. Aust., Malac. Section., no. 8, Muricidae, pl. 1, fig. 19.

Trophon (Litozamia) goldsteini Tenison-Woods. LUDBROOK, 1958, Trans. Roy. Soc. So. Aust., v. 81, p. 59, figs. 12, 13.

NOT *Litozamia goldsteini* (Tenison-Woods). KAICHER, 1980, Card Catalogue of world-wide shells, Pack no. 25 -Muricidae, Pt. 5, no. 2535 (= *Litozamia rudolphi*).

Description: Shell fusoid in outline, with seven teleoconch whorls and a protoconch of one and one-half smooth bulbous whorls. Spiral ornamentation of very faint striae, covering entire surface; on body whorl four to six vague spiral cords, best seen in specimens still covered by intritacalx. Axial ornamentation beginning on first post-nuclear whorl with six rounded varices that each cross the suture, overlapping the previous whorl; varical formation progressively abapertural, giving a backward curve to the varical line extending from spire to canal. Aperture oval, inner lip smooth, appressed; outer lip smooth, slightly patulous; no trace of an anal canal; siphonal canal short, broad, partially covered by a shelly plate but open by a narrow slit, recurved at distal end. When fresh exterior surface completely covered by a thick, pale brown intritacalx, having a linen-like texture; when eroded the remnant intritacalx remaining between spiral threads giving a frosted white appearance. Colour beneath the intritacalx white except for two faint brown bands, one at the suture and one at base of the body whorl. Radula typically muricine, with a rachidian plate having three major cusps, alternating with two minor cusps.

Type material: Tasmanian Museum TM 5241 (two syntypes, E823-8164) (T.A. Darragh, *in litt.* 24 Oct. 1983).

Type locality: Long Bay, Southern Tasmania.

Figured specimens: Australian Museum C.125234; height 18.5 mm, diameter 9.4 mm; locality: d'Entrecasteaux Channel, Tasmania (M. Ward Coll.) (Plate 1, fig. 5). Australian Museum C.125232; height 21.0 mm, diameter 10.0 mm; locality: Eden, NSW (N. Buckland Coll.) (Plate 1, fig. 6).

Discussion: Although one of the characteristics distinguishing the subgenus *Takia* from *Dermomurex* s.s. is the retention of six varices throughout the development of the shell, there is also an elongation of the siphonal canal and a reduction of spire height that gives the shell a very different appearance. The two living Australian species *D. goldsteini* and *D. angustus* do have six varices but the overall shape and appearance of the shell is much more akin to *D. scalaroides*, type of the genus (see pl. 1, fig. 10). For this reason, even though they have six varices they will be retained in *Dermomurex* s.s.

Winston Ponder, of the Australian Museum, has prepared a radula of *D. goldsteini* and it is typical of the *Dermomurex* group, which in turn is typically muricid. Radwin and D'Attilio (1976, text fig. 23) have illustrated the radula of *D. obeliscus* (A. Adams, 1853), showing the similarity to

other members of the subfamily Muricinae, in contrast to the subfamily Trophoninae, as illustrated in their text-figures 121 (*Boreotrophon clathratus*) and 132 (*Trophon geversianus*).

As noted above, all of the illustrations of this species leave much to be desired. That of Cotton (1956) shows denticulations on the inner side of the apertural lip, which, so far as the writer is aware, do not occur in this species. Likewise, Ludbrook's illustration (1958) shows what seems to be a two and one-half whorl protoconch when, in fact, the species has a one and one-half whorl protoconch, as do most other species of *Dermomurex*. However, as she notes, all of her specimens were more or less eroded and this may be the explanation for the appearance of the figured example.

Ludbrook (1958, p. 59) reported this species from the Pliocene Dry Creek Sands of South Australia. In addition, in material from the collections of the Western Australian Museum sent to the writer for study, there is a single specimen (no. 79.1530) from the Grange Burn Coquina (Kalimnan) at Hamilton, Victoria. Thus, *D. goldsteini* was widely distributed in southern Australia during Pliocene time.

The only available information suggests this is a relatively common species, found in depths of about 10-20 fathoms (18-36 m) along the southeastern corner of Australia (Tasmania, South Australia, to southernmost New South Wales).

DERMOMUREX (DERMOMUREX) ANGUSTUS (Verco, 1895)

Plate 1, figs. 8, 9

Trophon angustus VERCO, 1895, Trans. Roy. Soc. So. Aust., v. 19, p. 86, pl. 1, figs. 6, 6a (said to be 5, 5a).

Litozamia angusta (Verco). COTTON, 1956, Publ. Roy. Soc. So. Aust., Malac. Sect., no. 8, Muricidae, pl. 1, fig. 18.

Description: Shell narrowly fusoid in outline, with six teleoconch whorls and a protoconch of one and one-half smooth, bulbous whorls. Spiral ornamentation of fine striae covering entire surface, on body whorl five broad, obsolete spiral cords, most marked adjacent to varices. Axial ornamentation on each whorl of six low, rounded varices, each formed slightly abaperturally relative to the corresponding varix on previous whorl, giving a faintly sinuous curve to the varical line extending from spire to canal. Aperture elongate-oval, inner lip smooth, appressed; outer lip smooth, slightly patulous; siphonal canal short, broad, almost straight, partially covered over by a shelly plate but open by a narrow slit. Exterior of shell covered by a thick, chalky intritacalx, almost smooth when fresh but when slightly worn, coarse and fine axial lines and numerous spiral incisions becoming visible. Colour dirty white; animal unknown.

Type material: South Australian Museum D13482 (two paratypes); holotype not found.

Type locality: St Vincent Gulf, South Australia.

Figured specimens: Paratype A, South Australian Museum D13482(A); height 10.3 mm, diameter 4.5 mm (Plate 1, fig. 8). Paratype B, South Australian Museum D13482(B), height 10.6 mm, diameter 4.5 mm (Plate 1, fig. 9). Locality of both, St Vincent Gulf, "dredged in deep water."

Discussion: *Dermomurex angustus* is seemingly a rare shell, presumably because of its deeper habitat. No material other than the two figured paratypes are known to the writer. According to Verco the original type lot consisted of three specimens, two live, one dead. Presumably paratype A is the dead shell, paratype B is one of the live specimens and the holotype, which Verco stated was in his collection, was the second live one. The present location of the latter is not known to the writer.

As Verco noted, this species is differentiated from the closely related *D. goldsteini* by being smaller and more slender in overall shape. The ratio of width to height is about 0.5:1 in *D. goldsteini*, and 0.4:1 in *D. angustus*. Otherwise, there is little difference and, like *D. goldsteini*, it is also here assigned to *Dermomurex* s.s. in spite of the presence of six varices in the adult stage.

Subgenus **TAKIA** Kuroda, 1953

Takia KURODA, 1953, *Venus*, v. 17, no. 4, p. 190.

Type-species: *Murex inermis* Sowerby, 1841, by original designation (*non Murex inermis* Philippi, 1836, nec *M. inermis* Dujardin, 1837 [?=Philippi]) = *Dermomurex (Takia) infrons* Vokes, 1974.

DERMOMUREX (TAKIA) CRETACEUS E.H. Vokes, sp. nov.

Plate 2, figs. 4-6

Description: Shell fusoid in outline; protoconch of one and one-half smooth, cylindrical whorls, six teleoconch whorls. Spiral ornamentation extremely weak, not visible until third post-nuclear whorl, with one cord just posterior to suture; gradually adding a second at shoulder; on body whorl three cords, strength of these varying greatly between individuals, some almost smooth; only on body whorl very faint threads between major cords. Axial ornamentation beginning with six to eight small flanges that overlap onto protoconch on first post-nuclear whorl, becoming rib-like varices with the same number on each succeeding whorl. At intersection of axial varices and spiral cords small reflected protrusions developed, that at shoulder the largest. Strength of varices variable, some individuals with simple swollen ridges, others with distinct rib-like varices; no pattern apparent but usually all alike on any one specimen. Aperture elongate-oval, parietal lip narrow, smooth, appressed along entire length, bending into outer lip; latter usually also smooth but rarely having five small denticles; lip curved into reflected protrusion at shoulder and posterior portion slightly patulous. Siphonal canal long, recurved into a continuous curved line, forming a faint umbilical chink. In life, presumably covered with a thick intritacalx, this usually more or less lost in the fossil state, leaving behind a pattern of spiral tunnels visible over the entire shell exterior.

Holotype: National Museum of Victoria P 74140; height 24.6 mm, diameter 11.7 mm (Plate 2, fig. 4).

Paratype A: South Australian Museum P 23844; height 18.3 mm, diameter 9.5 mm (Plate 2, fig. 5).

Paratype B: Australian Museum C.139791; height 11.5 mm, diameter 6.4 mm (Plate 2, fig. 6).

Other material studied: National Museum of Victoria, specimens numbered P 74093-144, from Glen Aire Clay ("Late Aldingan", i.e. early Oligocene), Pt Flinders, near Cape Otway; collected by T.A. Darragh and T. Hughes (P 74093-104) or F.A. Cudmore (P 74105-144).

Type locality: Glen Aire Clay (early Oligocene), Pt Flinders, near Cape Otway, Victoria.

Discussion: As noted in the Introduction, this new species is extremely common in the early Oligocene Glen Aire Clay*. Although it is clearly of the *Takia* group, it differs from the type of the subgenus, *D. infrons*, in being more angulate, with a strong fold at the shoulder of the shell. It most nearly resembles the recently described *Takia bobyini* Kosuge (1984, p. 144, pl. 50 figs. 1, 2 — fig. 1 reproduced here, pl. 2, fig. 7) from deep water in the Philippines. The Australian species differs from the Philippine one in having only three major spiral cords in place of the four in the Recent form and in having a less inflated body whorl.

The name "*Trophon cretaceus*" was first cited by Tate (*in* Tate and Dennant, 1895, p. 111) in a list of fossils from Cape Otway. It is assumed that Dr Darragh recognised the derivation of the name, in reference to the intritacalx, and applied it to the species in the Museum collections. Certainly there could be no more appropriate epithet, and it is with pleasure that the writer adopts the manuscript name of Tate.

*In the museum collections there are also another four juvenile specimens (P 74078, P 74090-92), collected by F.A. Cudmore from the Janjukian beds at Bird Rock Cliff, Torquay. Although they may be referable to *D. cretaceus*, they are too immature to be positive. Inasmuch as they do not occur in the same formation as the typical form, the writer prefers to await the discovery of adult material before stating that the species also occurs in the Jan Juc Formation.

DERMOMUREX (TAKIA) IMITATOR E.H. Vokes, sp. nov.

Plate 2, fig. 1

Description: Shell with protoconch of one and one-quarter smooth bulbous whorls, larger than succeeding post-nuclear whorl; teleoconch with five whorls in unique holotype, probably six in adult stage. Spiral ornamentation not developed until approximately second post-nuclear whorl with initially a single strong cord immediately posterior to suture, developing a second cord at the shoulder on third post-nuclear whorl; the two cords continuing through penultimate whorl, four strong cords on body whorl, the anteriormost not quite as strong as the others; one additional weaker cord on subsutural area and another at base of the body whorl; between these stronger cords extremely faint spiral threads, best seen on the body whorl. Axial ornamentation beginning with a small sharp varix marking the change from proto- to teleoconch; eight ridges on each post-nuclear whorl, becoming increasingly heavy and cord-like with growth; on fourth postnuclear whorl every third ridge becoming a true varix, with intervening ridges remaining as intervarical ribs, of the same size as the varices; by fifth whorl every ridge becoming a true varix, eight in all on body whorl. At intersection of axial ridges and spiral cords pointed nodes developed, their size proportional to the strength of the cord. Whorls greatly inflated; suture deeply impressed, crossed by the varical ridges abutting against the previous whorl. Aperture large, ovate; smooth, heavy parietal lip, free-standing anteriorly, appressed posteriorly and curving smoothly into the outer lip, the latter having five weak denticulations on the slightly patulous anterior half. Siphonal canal moderately long, open by a narrow slit, recurved at the distal end; terminations of previous canals fitting within each other, giving rise to a marked umbilical chink. Shell surface almost completely smooth except for spiral cords and extremely weak threads; in life the exterior presumably covered with a heavy deciduous intritacalx, only traces remaining in holotype.

Holotype: National Museum of Victoria P 74074; height 28.4 mm, diameter 19.6 mm (Plate 2, fig. 1).

Type locality: Jan Juc Formation (Janjukian); "The Ledge," Bird Rock Cliff, Torquay, Victoria (F.A. Cudmore Coll.).

Discussion: This remarkable new species from the Jan Juc Formation is superficially identical to the American *D. sexangulus* (Dall, 1915) from the latest Oligocene-earliest Miocene Silverdale Beds of North Carolina. However, the American species has a relatively small protoconch, approximately one-half the diameter of the very large protoconch of the Australian species (see pl. 2, fig. 1c) and from the first post-nuclear whorl has six true varices on every whorl. The Australian shell initially has eight ridges per whorl, which become true varices only on the fourth and fifth post-nuclear whorls. The denticulations on the inner lip of the American shell are somewhat stronger and more numerous, extending over the entire inner lip in some specimens. However, in some examples they are no different from the unique Australian shell and so more material may remove this apparent distinction. Regardless, the overall appearance of the two species is incredibly similar and they must be the result of parallel development from a not too distant common ancestor, presumably in the Tethyan area.

When the writer separated the new subgenus *Viator* from the ancestral line of *Takia* (Vokes, 1974a, p. 2) she assigned the American species *D. sexangulus* to *Viator* as well, on the assumption that it was directly ancestral to the *Viator* line. However, the discovery of this new, more reasonable, ancestor in the Australian Tertiary caused a re-evaluation of the position of *D. sexangulus*. Both *D. sexangulus* and *D. imitator* have the relatively short recurved, siphonal canal and the large inductura of typical *Takia*, in contrast to the long straight canal and small inductura of *Viator*. Therefore, it is deemed preferable to return *D. sexangulus* to *Takia*, relegating the development of *Viator* entirely to the Australasian region. The other American species, *D. vaghani* (Maury, 1910) and *D. curvductus* Vokes, 1975, as well as the Italian *D. taurinensis* (Michelotti, 1841) (all figured in Vokes, 1975), should also be returned to *Takia*, as they have more affinities with the ancestral line than with the derivative one (even though one must admit *D. vaghani* with its straight canal is another interesting example of convergence).

DERMOMUREX (TAKIA) PACHYSTIRUS (Tate, 1888)

Plate 2, fig. 3

Murex (Rhinocantha) pachystirus TATE, 1888, Trans. Roy. Soc. So. Aust., v. 10, p. 102, pl. 2, fig. 11.*Bolinus pachystirus* (Tate). COTTON, 1956, Publ. Roy. Soc. So. Aust., Malac. Section, no. 8, Muricidae [p. 1]*[Aspella] (Takia) pachystirus* (Tate). VOKES, 1971, Bulls. Amer. Paleont., v. 61, no. 268, p. 78.*Dermomurex (Takia) pachystirus* (Tate). VOKES, 1974, J. Malac. Soc. Aust., v. 3, no. 1, p. 7; 1975, Tulane Stud. Geol. Paleont., v. 11, no. 3, p. 127.

Description: Shell inflated biconical, with five teleoconch whorls and a protoconch of one and one-half smooth, bulbous whorls. Spiral ornamentation beginning with a single weak cord at the periphery, others gradually intercalated; body whorl with six weak spiral cords, visible primarily where they cross the varices, that cord at the periphery causing a marked angulation of the whorl; surface otherwise marked only by faint spiral striae. Axial ornamentation from first teleoconch whorl consisting of six low, ridge-like varices, marked only by the spiral cords and placed alternately with the corresponding varices of the preceeding whorl eliminating any continuity of varical line from spire to canal. Suture deeply impressed, strongly sinuated by alternation of varices. Aperture large, angulate, inner lip smooth, narrow, appressed along the entire length; outer lip weakly lirate within. Siphonal canal long, almost straight but slightly recurved at distal end; open by a narrow slit. In life entire exterior surface covered by a thick intritacalx, usually lost in fossil state, with only remnant patches remaining.

Holotype: South Australian Museum (AUGD) T 410.**Type locality:** Murray River, south of Morgan, South Australia.

Figured specimen: Holotype, South Australian Museum (AUGD) T 410; height 24 mm, diameter 15.5 mm (*vide* Tate, 1888); locality, Cadell Marl (Balcombian), Murray River Cliffs, 5.8 km south of Morgan (Tate, 1888, p. 172; Ludbrook, 1973, p. 251) (Pl. 2, fig. 3).

Discussion: According to Tate (1888, p. 103) this species occurs in the lower beds at Muddy Creek (Muddy Creek Marl, Balcombian) and in the "Gastropod-bed, River Murray Cliffs, near Morgan" (Cadell Marl Member of the Morgan Limestone, see Ludbrook, 1973, p.251). It must be a rare species as there is but one other specimen in the collections of the National Museum of Victoria and no others known to the writer.

The shape of the outline in this species is unlike any other member of the subgenus *Takia* presently known. The body whorl is extremely inflated, with a marked angulation at the periphery of the shell rather than at the shoulder, as in the previous species. The suture is deeply impressed, with the varical ridges causing it to be strongly sinuated. As with *D. imitator* and *D. sexangulus*, the aperture is denticulate.

Tate placed this species in the subgenus *Rhinocantha*, a synonym of *Bolinus* Pusch, 1837 (type: *Murex brandaris* Linné, 1758), but the resemblance is only superficial. The writer (Vokes, 1963, p. 151) made the same mistake when she referred the American *D. vaughani* (Maury) to "*Murex (Bolinus)*" because of the same sort of confusion. The two groups are only distantly related and the resemblances are due purely to convergence; the Miocene ancestral species of *Bolinus* do not have any similarity to the Miocene members of *Takia*. But when all of the intritacalx is removed from a *Takia*, as it so often is in the fossil state, then the similarity to the Recent Mediterranean *Murex brandaris* is remarkable.

DERMOMUREX (TAKIA) GLEBOSUS E.H. Vokes, sp. nov.

Plate 3, figs. 5-7

Description: Shell biconic in outline; six teleoconch whorls and a protoconch of one and one-quarter smooth, bulbous whorls, tip immersed. Spiral ornamentation beginning on first post-nuclear whorl, consisting of only extremely faint threads superimposed upon indistinct larger cords; on early whorls one cord at shoulder, a second at periphery, and a weaker third on subsutural ramp; on body whorl five or six such cords, plus an additional five or six on the extended siphonal canal.

Axial ornamentation beginning on first post-nuclear whorl, consisting of rounded varices, unornamented except for a moderately strong angulation at the shoulder; five or six per whorl, but always the same number on each whorl of any given specimen (i.e., all five or all six). Suture appressed but crossed by varices abutting corresponding varix on previous whorl, placed abaperturally giving a backward spiral to varical line from apex to canal. Aperture oval; inner lip smooth, appressed; outer lip slightly patulous at anterior half, with about five indistinct nodes on inner edge. Siphonal canal moderately long, open by a narrow slit, recurved at distal end, forming a small umbilical chink. In life covered by an extremely thick intritacalx but invariably lost in fossil state, only small remnant patches remaining.

Holotype: Western Australian Museum 84.601; height 28.8 mm, diameter 15.2 mm (Plate 3, Figure 5).

Paratype A: Western Australian Museum 84.602; height 6.3 mm, diameter 2.8 mm (Plate 3, figure 6).

Paratype B: Australian Museum C. 90093; height 28.8 mm; diameter 14.8 mm (Plate 3, figure 7).

Other material studied: Western Australian Museum 80.230 (12 specimens), 80.214 (8 specimens), both from basal 0.4 m of pit; nos. 81.1726, 80.243 (1 each), both from spoil on floor of pit; 81.1035 (4 specimens), from basal 0.6 m of pit; collected by V.A. Ryland, G.E. and W.E. Kendrick; locality of all same as type locality.

Type Locality: Roe Calcarenite (Pliocene), Roe Plains, pit 0.5 km north of Hampton Repeater Tower; Madura District, Western Australia.

Discussion: In the Roe Calcarenite of Western Australia there are numerous specimens of a large species that in general appearance is most nearly akin to *D. cretaceus*, described above, and the recently described *D.(T.) bobyini* (Kosuge) from the Philippine Islands. But it differs from both of these in having a more massive, more heavily ornamented shell; hence the specific name (*glebosus*, Latin — lumpy). These three species share the angulate shoulder not seen in any other species of *Takia*.

In her original study of the mollusks of the Roe Calcarenite, Ludbrook (1978) concluded that, because of the large number of extant species, the age was early Pleistocene. However, George W. Kendrick of the Western Australian Museum, who is working on the fauna of the Roe, considers the age to be Pliocene (*in litt.*, 31 August 1982). Although Mr Kendrick is studying the fauna of the Roe, he graciously allowed the writer to include this species in her study.

Subgenus VIATOR Vokes, 1974

VIATOR VOKES, 1974, J. Malac. Soc. Aust., v. 3, no. 1, p. 4.

Type species: *Dermomurex (Viator) antonius* Vokes, 1974, by original designation.

DERMOMUREX (VIATOR) DARRAGHI E. H. Vokes, sp. nov.

Plate 3, figs. 3, 4.

Description: Shell moderately large, protoconch of one and one-half smooth, bulbous whorls, six teleoconch whorls in adult. Spiral ornamentation primarily developed in the deciduous intritacalx, beneath this just a single cord at periphery on early whorls, very faint secondary threads gradually added; on body whorl four or five stronger cords, that at the shoulder weakest; between cords only faint spiral threads crossed by equally faint axial growth striae, giving a cloth-like pattern to the shell surface. Axial ornamentation beginning with six or seven small rounded ribs on each whorl, gradually strengthening into varices but number remaining constant. Varices drawn out at shoulder into an upturned angulate process, with a small open flange present only at the shoulder; remainder of varix rounded and crossed by spiral cords. Suture deeply impressed, sinuated by varices abutting against varices of previous whorl. Aperture pyriform; inner lip narrow, smooth, appressed; curving into outer lip, also smooth within. Siphonal canal long, almost straight, only weakly recurved at distal end, with previous canals diverging as small spurs on some specimens, others neatly fused into a tube-like form, but open by a narrow slit on the abaxial side. In life covered by a thick intritacalx, in fossil examples only remnants, showing a series of tiny tunnels paralleling the spiral cords.

Holotype: National Museum of Victoria P 74086; height 18.5 mm, diameter 10.7 mm (Plate 3, fig. 3).

Paratype: National Museum of Victoria P 74083; height 19.0 mm, diameter 10.4 mm (Plate 3, fig. 4).

Other material studied: National Museum of Victoria P 74081, 74082, from Fishing Point Marl, lower horizon (Longfordian), cliff 10 m above Lake Craven, Aire River, SE of Fischers Point, Horden Vale, Victoria; P 74085, same as type locality. All specimens collected by T.A. Darragh and H.E. Wilkinson.

Type locality: Gellibrand Clay (Batesfordian), Cobden-Lavers Hill Road, cut 1 km south of turnout to Kennedy's Creek, north of Princetown, Victoria.

Discussion: In the collections of the National Museum of Victoria there are five specimens of a species that is closely related to the slightly younger (Balcombian) *D. asteriscus*. From the latter this new species differs in having a more elongated siphonal canal and less inflated body whorl. The inner side of the outer lip, so far as the available material shows, lacks the denticulations of *D. asteriscus*. In many ways the shell more nearly resembles the Recent *D. antonius*, but differs from that species also in the lack of labral denticles.

The writer takes pleasure in naming this species in honour of Dr Thomas A. Darragh, of the National Museum of Victoria, for his extensive work on the Tertiary of Australia. He collected not only the material upon which this species is based but most of the other fossil material utilized in this entire paper.

DERMOMUREX (VIATOR) ASTERISCUS (Tate)

Plate 3, figs. 1, 2

Murex (Rhinocantha) asteriscus TATE, 1888, Trans. Roy. Soc. So. Aust., v. 10, p. 102, pl. 2, fig. 10.

Bolinus asteriscus (Tate). COTTON, 1956, Publ. Roy. Soc. So. Aust., Malac. Section, no. 8, Muricidae [p. 1].

[*Aspella*] (*Takia*) *asteriscus* (Tate). VOKES, 1971, Bulls. Amer. Paleont., v. 61, no. 268, p. 20.

Dermomurex (Viator) asteriscus (Tate). VOKES, 1974, J. Malac. Soc. Aust., v. 3, no. 1, p. 5, pl. 1, fig. 3; 1975, Tulane Stud. Geol. Paleont., v. 11, no. 3, pp. 127, 153, pl. 6, fig. 3.

Description: Shell very inflated with six teleoconch whorls and a protoconch of one and one-half large, bulbous whorls, terminating at a small sharp varix. Spiral ornamentation on early post-nuclear whorls of a single strong cord at the periphery, by third post-nuclear whorl a second cord added at shoulder; on body whorl six strong cords and an additional three or four on the extended siphonal canal; entire surface covered by very faint spiral striae. Axial ornamentation beginning on earliest post-nuclear whorls with six or seven rounded varices, these persisting in the same number on each successive whorl; varices increasing in strength on each whorl and undulated by the crossing of the spiral cords, especially at the shoulder where a small abapertural flange may be developed. Suture greatly impressed, crossed by varices abutting against the corresponding varix on preceeding whorl, but placed abaperturally, giving a backward spiral to the varical line from spire to canal. Aperture large, oval; inner lip smooth, slightly flaring at anterior end, appressed at posterior end and curving gently into outer lip; latter crenulated on outer margin, reflecting major spiral cords, about 12 small denticles within. Siphonal canal long, straight, successive canals sealed into a tube-like structure, almost closed but open by a narrow slit. In life entire surface covered by a thick intritacalx but usually lost in fossil state, with only remnant patches remaining.

Holotype: South Australian Museum (AUGD) T440B.

Type locality: Muddy Creek, west of Hamilton, Victoria.

Figured specimens: National Museum of Victoria P 74087; height 27.0 mm, diameter 18.8 mm (J. Dennant Coll.) (Plate 3, fig. 1). South Australian Museum (AUGD) T 440B (holotype); height 27 mm, diameter 19 mm (*vide* Tate, 1888) (Plate 3, fig. 2). Locality of both, Muddy Creek Marl (Balcombian), Muddy Creek, 8 km west of Hamilton, Victoria.

Discussion: As with *D. pachystirus*, this species was also placed in *Rhinocantha* (= *Bolinus*) by Tate. The writer (Vokes, 1971) originally considered it a member of the subgenus *Takia* (which she assigned to the genus *Aspella*, at the time), but the discovery of *D. antonius*, which is so clearly the living descendant of *D. asteriscus* caused a re-evaluation of the form, with subsequent placement in the newly erected subgenus *Viator* (Vokes, 1974a).

This species does not seem to be as rare as *D. pachystirus* with which it is said to occur, there are three examples in the collections of the National Museum of Victoria and another in the U.S. National Museum (that figured by Vokes previously in 1974a, 1975). But so far as known it occurs only at Muddy Creek.

DERMOMUREX (VIATOR) ANTONIUS Vokes

Dermomurex (Viator) antonius VOKES, 1974, J. Malac. Soc. Aust., v. 3, no. 1, p. 4, pl. 1, figs. 1, 2; 1975, Tulane Stud. Geol. Paleont., v.11, no.3, pp. 127, 153, pl. 6, figs. 4, 5.

Viator antonius (Vokes). FAIR, 1976, The Murex Book, p. 21, pl. 16, fig. 21.

Description: "Protoconch relatively large, 1½ bulbous whorls, slightly papillate; terminating at a pronounced crescentic varix. Six teloconch whorls in adult. Spiral ornamentation normally masked by intritacalx but when latter is removed the shell can be seen to be covered by numerous spiral cords of three orders of magnitude: moderately heavy cords, about six in number on the body whorl plus an additional three or four on the siphonal canal; between each pair of major cords, a slightly smaller spiral ridge and alternating with these a tertiary thread, so that the pattern formed is a typical muricine one of first order spiral, third order, second, third, first, repeated over the entire surface. On the spire three major spiral cords beneath the intritacalx. Axial ornamentation of six rounded varices per whorl, which extend the entire length of the anterior canal. Suture greatly impressed, crossed by the varices, which abut each previous whorl slightly abaxially to the corresponding varix. Aperture oval, with small, raised peristome, about seven indistinct denticles within the outer lip; inner lip smooth. Siphonal canal long, straight, with previous terminations fused into an almost smooth tube, nearly covered over by a thin plate extending from the columellar wall, but open by a narrow slit. Colour of shell a light brown but normally covered by the ivory-coloured intritacalx, which is a thick, spongy, deciduous, calcareous material that when unworn has the appearance of having a series of small perforations arranged in spiral rows over the entire external shell surface. When broken away, as it frequently is, the interior of this intritacalx can be seen honeycombed with fine tubes, in spiral lines circling the shell. Animal unknown; operculum muricoid with apical nucleus." (Vokes, 1974)

Holotype: Western Australian Museum 3646-67; height 25.7 mm, diameter 13.5 mm.

Type locality: Scholl Island, Dampier Archipelago, Western Australia.

Discussion: This unusual species, which was named as the type of a new subgenus when originally described, was based upon two specimens taken in 1960 by the King-Western Australian Expedition in the Dampier Archipelago. Although the paratype came from only 42 metres depth (no data on the holotype), to the writer's knowledge no additional specimens have been found since the initial collection. Thus, there is nothing to be added to the original discussion, wherein it was noted that this species was obviously the living descendant of the Miocene *D. asteriscus*, differing from that form only in having a more diverse spiral ornamentation, a smaller aperture, and a longer siphonal canal. In the two latter aspects it more nearly resembles the new species described above as *D. darraghi*, which is however somewhat older (Longfordian — early Miocene) than *D. asteriscus* (Balcombian — middle Miocene).

ACKNOWLEDGEMENTS

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Gackle, of the South Australian Museum, provided the photographs of Tate's and Verco's types (both those published herein and others that were not used). Joseph Rosewater, U.S. National Museum, loaned a Recent specimen for figuring; George W. Kendrick, Western Australian Museum, provided material from the Roe Calcarenite; and W.H. Akers, Chevron Oil Field Research Company, determined a critical age date; to all of these persons she is extremely grateful. The manuscript was greatly improved by the suggestions of both Dr Darragh and Dr Myra Keen, Stanford University (Emeritus).

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PLATE 1

Figures

1-4. *Dermomurex (Dermomurex) garrardi* E.H. Vokes, sp. nov.

1. (X 4) National Museum of Victoria P 74477 (holotype); height 16.0 mm, diameter 6.5 mm
2. (X 4) Australian Museum C.131237 (paratype A); height 13.4 mm, diameter 5.2 mm
3. (X 4) South Australian Museum P 23845 (paratype B); height 11.6 mm, diameter 5.0 mm
4. (X 4) Australian Museum C.131237a (paratype C); height 11.0 mm, diameter 5.5 mm

Locality of all: Fossil Beach, Balcombe Bay, Victoria

5, 6. *Dermomurex (Dermomurex) goldsteini* (Tenison-Woods)

5. (X 3) Australian Museum C.125234; height 18.5 mm, diameter 9.4 mm

Locality: d'Entrescasteaux Channel, Tasmania

6. (X 2¼) Australian Museum C.125232; height 21.0 mm, diameter 10.0 mm

Locality: Eden, New South Wales

7. *Dermomurex (Trialatella) neglecta* (Habe and Kosuge)

- (X 2) Vokes Coll.; height 22.4 mm, diameter 11.9 mm

Locality: Bonin Islands, 200 metres

8, 9. *Dermomurex (Dermomurex) angustus* (Verco)

8. (X 3) South Australian Museum D13482(A) (paratype A); height 10.3 mm, diameter 4.5 mm.
9. (X 3) South Australian Museum D13482(B) (paratype B); height 10.6 mm, diameter 4.5 mm

Locality of both: St Vincent Gulf, deep-water.

NOTE: These photographs are reproduced by the courtesy of the South Australian Museum

10. *Dermomurex (Dermomurex) scalaroides* (Blainville)

- (X 3) U.S. National Museum 89092; height 18.0 mm, diameter 8.8 mm

Locality: Sicily

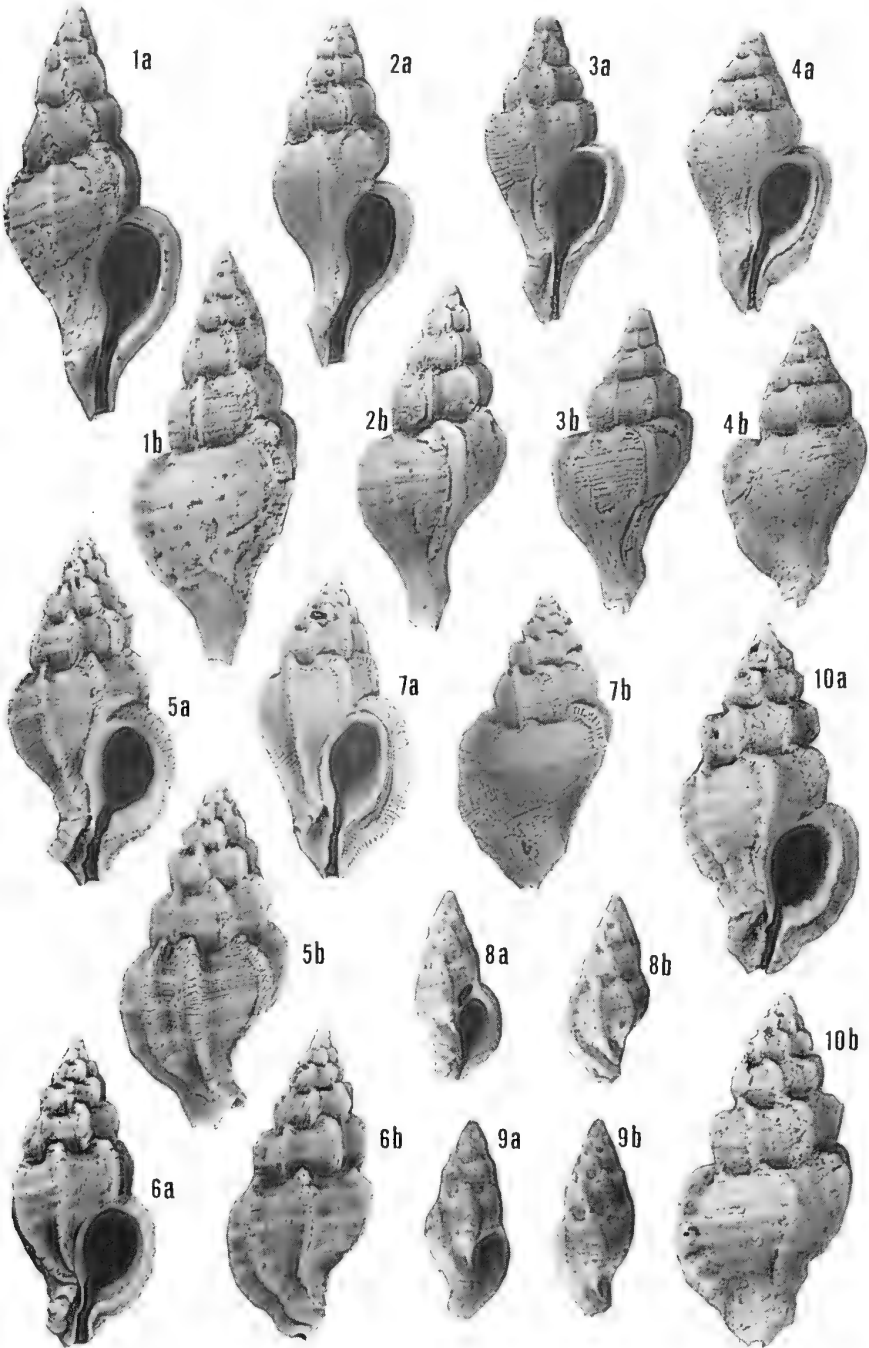


PLATE 2

Figures

1. *Dermomurex (Takia) imitator* E.H. Vokes, sp. nov.
(X 1½) National Museum of Victoria P 74074 (holotype); height 28.4 mm, diameter 19.6 mm
Locality: Bird Rock Cliff, Torquay, Victoria
2. *Dermomurex (Takia) sexangulus* (Dall)
(X 1½) U.S. National Museum 644377; height 43.5 mm, diameter 26.0 mm
Locality: Silverdale, North Carolina, USA
3. *Dermomurex (Takia) pachystirus* (Tate)
(X 2) South Australian Museum (AUGD) T410 (holotype); height 24 mm, diameter 15.5 mm
Locality: Murray River Cliffs, near Morgan, South Australia
NOTE: These photographs are reproduced by the courtesy of the South Australian Museum
- 4-6. *Dermomurex (Takia) cretaceus* Vokes, sp. nov.
 4. (X 3) National Museum of Victoria P 74140 (holotype); height 24.6 mm, diameter 11.7 mm
 5. (X 3) South Australian Museum P 23844 (paratype A); height 18.3 mm, diameter 9.5 mm
 6. (X 4) Australian Museum C.139791 (paratype B); height 11.5 mm, diameter 6.4 mm
Locality of all: Pt Flinders, Cape Otway, Victoria
7. *Dermomurex (Takia) bobyini* (Kosuge)
(X 2) Paratype, collection of Victor Dan; height 27.7 mm, diameter 12.2 mm (reproduced from Kosuge, 1984, pl. 50, fig. 1).
Locality: Panglao, Bohol, Philippines, 120 fms. (=220 m).

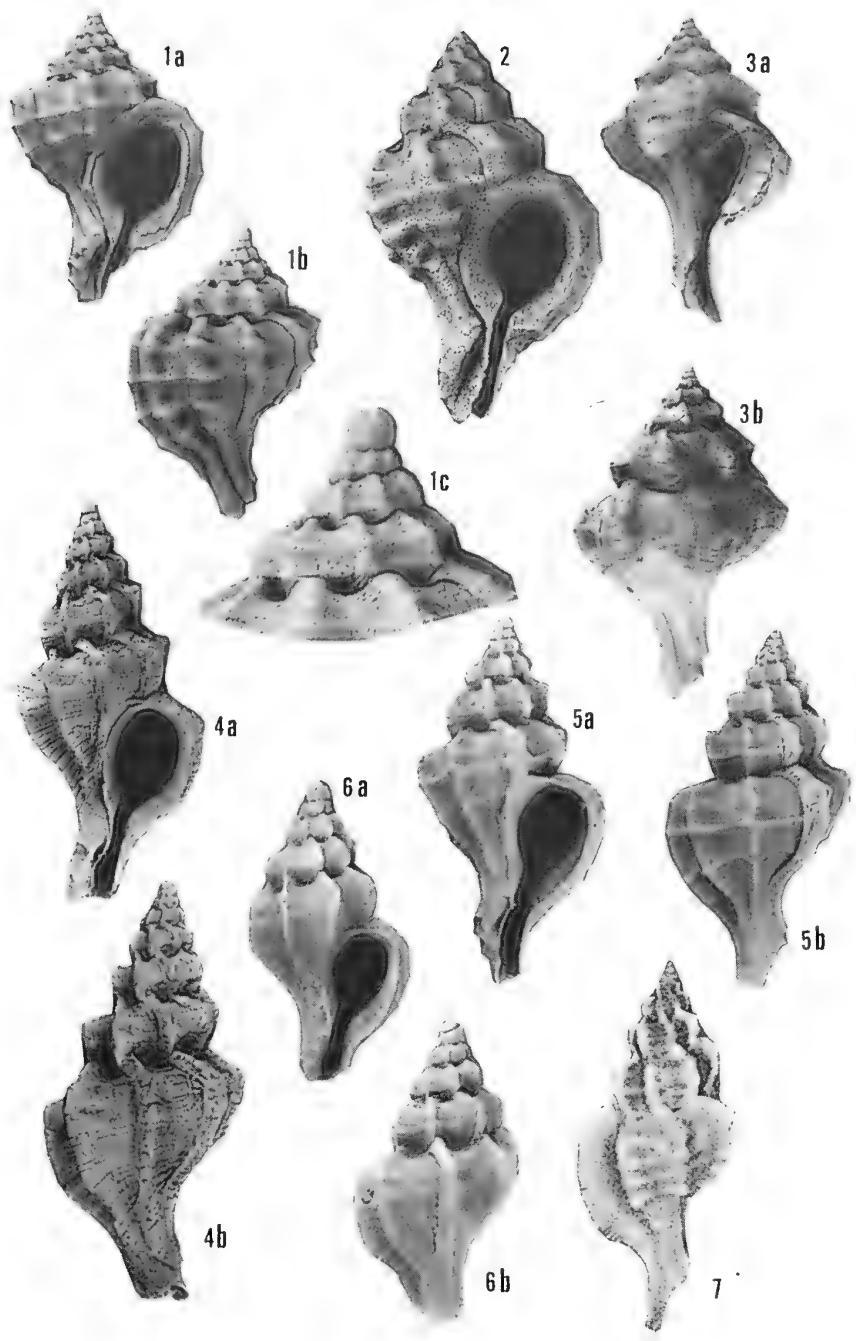


PLATE 3

Figures

1, 2. *Dermomurex (Viator) asteriscus* (Tate)

1. (X 2) National Museum of Victoria P 74087; height 27.0 mm, diameter 18.8 mm

2. (X 2) South Australian Museum (AUGD) T 440B (holotype); height 27 mm, diameter 19 mm (*vide* Tate, 1888)

NOTE: These photographs are reproduced by the courtesy of the South Australian Museum
Locality of both: Muddy Creek, Hamilton, Victoria.

3, 4. *Dermomurex (Takia) darraghi* Vokes, sp. nov.

3. (X 3) National Museum of Victoria P 74086 (holotype); height 18.5 mm, diameter 10.7 mm
Locality: Cobden-Lavers Hill Rd., Victoria

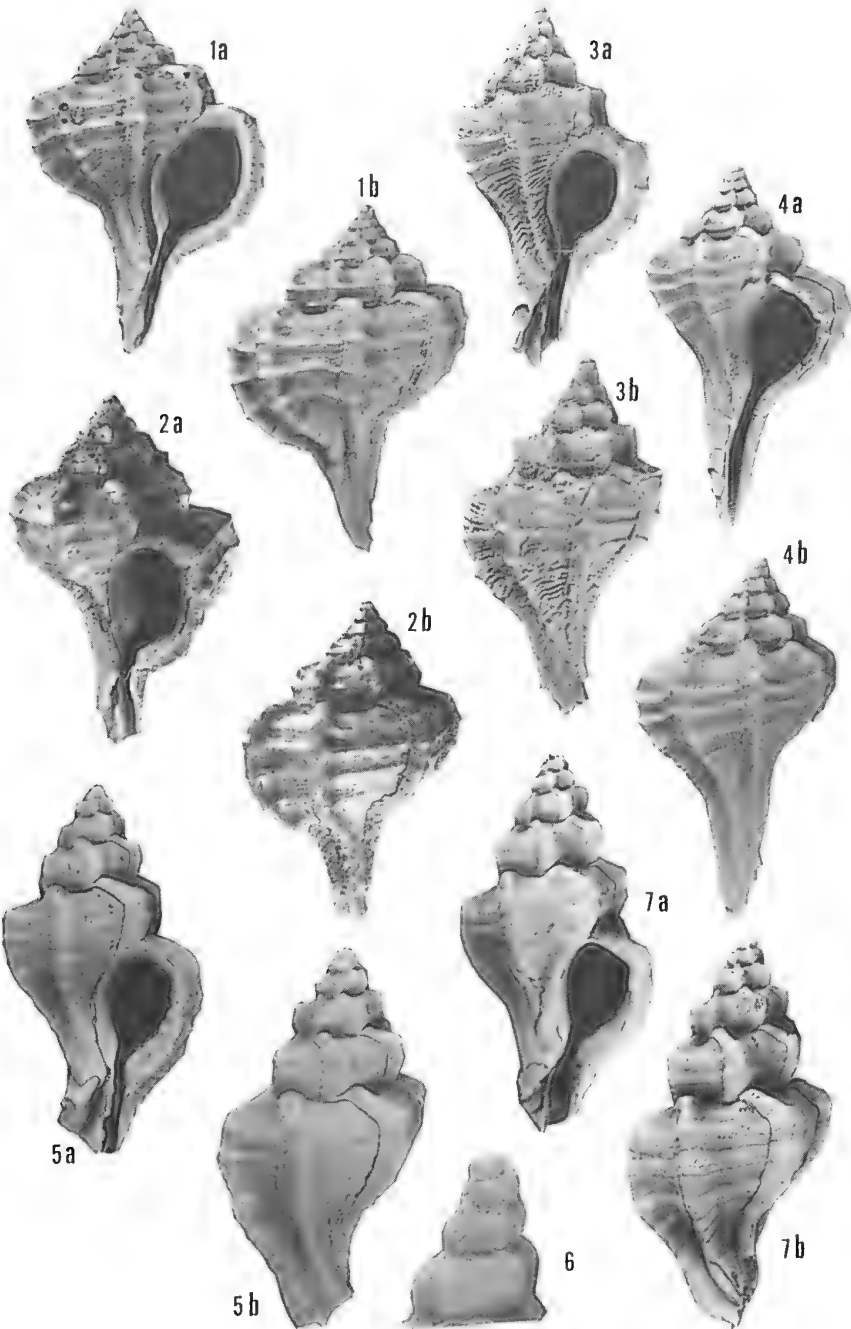
4. (X 3) National Museum of Victoria P 74083 (paratype); height 19.0 mm, diameter 10.4 mm
Locality: Lake Craven, Horden Vale, Victoria

5-7. *Dermomurex (Takia) glebosus* Vokes, sp. nov.

5. (X 2) Western Australian Museum 83.601 (holotype); height 28.8 mm; diameter 15.2 mm

6. (X 10) Western Australian Museum 84.602 (paratype A); height 6.3 mm, diameter 2.8 mm

7. (X 2) Australian Museum C.90093 (paratype B); height 28.8 mm, diameter 14.8 mm
Locality of all: Roe Plains, Madura District, Western Australia.





Murexiella perculata, sp. nov.
(Gastropoda:Muricidae), from the Miocene of
Victoria

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ABSTRACT

Murexiella perculata, sp. nov., from the middle Miocene of Victoria, is the first recorded occurrence of the genus *Murexiella* s.s. in the fossil record of Australia. Comparison is made with the Pliocene-Recent group of *Murexiella* (*Subpterynotus*) and it is concluded that this new species is not in the line of the latter group, but is most nearly related to the ancestral *Murexiella* s.s. species, such as *M. steuri* (Cossmann), from the middle Eocene of France.

INTRODUCTION

Some time ago the writer (Vokes, 1974) published a paper on the subject of Recent species of Australia that seemed to be most nearly related to fossil forms found in the Tertiary of the Western Atlantic. This paper was written with the full knowledge that in time intermediate species would be discovered that would prove there was no validity to what she was suggesting but little did she anticipate that she would be the one to discover them. However, an extended visit to Australia during the last half of 1980 permitted both a study of collections at the Australian Museum and an all too brief collecting trip to classic Tertiary localities, such as Fossil Beach and Muddy Creek, in Victoria. The result of these activities was recognition of a number of new fossil muricids, some of which are being described in an accompanying article and another that is described herein.

The muricid genus *Murexiella* is one of the first genera to be developed in that family, being known from beds as old as middle Eocene in both the United States and France. In the Recent fauna there are numerous species known from all parts of the tropical world, including Australia (see Ponder, 1972).

In the typical *Murexiella* (type species: *Murex hidalgoi* Crosse, 1869; Recent, Caribbean) the varices (which number from four to seven) are ornamented by more or less long fingerlike processes, connected by elaborately laminated webbing. The siphonal canal is moderately short and is ornamented only by the elongate processes, sans webbing. In the subgenus *Subpterynotus* (type species: *Murex textilis* Gabb, 1873; Miocene, Dominican Rep.) the varices may be reduced to three in number in the adult; the digitations are reduced in relative size and are webbed to the tips; the webbing continues down the length of the siphonal canal. Thus, the Australian species

Murex tatei Verco, 1895, in the Recent fauna, and *Homalocantha antedecens* Ludbrook, 1958, from the Pliocene, have both been referred to *Murexiella* (*Subpterynotus*). (See Vokes, 1974, for further discussion and illustrations of the pertinent species.) However, the Australian species differ from the typical *Subpterynotus* in ways that indicate they are closer to the ancestral *Murexiella* morphotype. The siphonal canal is not so elongated and there are more than three varices on the adult body whorl. This suggests that the resemblance of the Pliocene and Recent Australian species to the American *Subpterynotus textilis* may only be due to convergence.

The problems of convergence in the Muricidae is one that is a continual complication. Repeatedly we see totally different lines gradually evolving to amazingly similar end products. The most notable example is in the *Pterynotus-Pteropurpura* groups, which (although in different subfamilies) have a shell morphology that confused workers for years until the differences in the radula, operculum, and even shell composition (aragonite vs. calcite) were recognised. There is now good evidence (D'Attilio, 1982) that the various genera united into the subfamily Typhinae, due to the presence of the "characteristic" tubes, may be only distantly related and the entire "group" may be a massive case of convergence. The similarity of the spinose shells of *Murex* s.s. and some members of the subgenus *Chicoreus* (*Siratus*) are certainly, once again, only due to convergence.

So the possibility that the Australian and American members of *Subpterynotus* are not closely related is real. But the very finely laminated ornamentation in the Australian and American species referred to *Subpterynotus* is amazingly similar and unlike the typical *Murexiella*. Both have an elongated canal, with the webbing continuing down the full length of this canal (if anything, more well-developed in the Australian species than in the American one). In contrast, the newly-found Miocene Australian species *M. perculata* is more akin to the typical *Murexiella* species, especially such Eocene forms as "*Murex*" *stueri* Cossmann, 1889 (see p1. 1, fig. 7), than to the *Subpterynotus* morphotype. There is no compelling evidence other than geography to indicate that the Miocene species is, in fact, ancestral to the younger ones.

Superficially *M. perculata* bears the strongest resemblance to members of the genus *Homalocantha*, especially the living Australian *H. secunda* (Lamarck, 1822). But there is one marked difference between all members of *Homalocantha* and this new species and that is the presence of a large partition, or varical flange, above the aperture, crossing the suture at each varix. It is this shell character that permits us to distinguish between the otherwise remarkably similar shells of two genus-groups, which are extremely different in both radular and opercular characters.

Homalocantha Mörch, 1852 (type species: *Murex scorio* Linné, by monotypy), is certainly derived from the older *Murexiella*; however, it may be distinguished by the presence of a purpuroid operculum (with a lateral nucleus) and a muricoid radula, in contrast to the three-dimensional muricopsine radula of *Murexiella*. The earliest known species of *Homalocantha* is apparently "*Murex*" *pauli* Tournouer in Benoist, 1880, which Cossmann and Peyrot (1923, p. 126, pl. 13, figs. 40,41) state occurs in the Burdigalian and possibly in the Aquitanian (based upon a single juvenile example) of France. In the Aquitanian of the United States there is another species very like *H. pauli* but even more similar to the Australian *M. perculata*. The American "*Murex*" *crispangula* Heilprin, 1887 (here figured, pl. 1, fig. 6) differs from the European "*M.*" *pauli* in that the latter has four major spiral cords separated by sets of alternating secondary and tertiary threads but the American species has six such major cords, with the result that all of the ornamentation is reduced in size, even though the three orders of magnitude are still present.

The six major spiral cords create a strong air of resemblance between the American and the Australian shells but there is no trace of a partition in *M. perculata*. Once again we must invoke convergence in the two lines: one, the American "*M.*" *crispangula*, which may be the first *Homalocantha*; and another, the Australian *M. perculata*, which only superficially looks like *Homalocantha*.

In most species of Muricidae there are three orders of spiral ornamentation: primary major spiral cords separated by alternating secondary and tertiary threads, in a pattern of primary, tertiary, secondary, tertiary, primary. This pattern appears to be reduced in *M. perculata* and, looking directly at the shell, it seems to have only primary and secondary ornament. But the tertiary threads are present on the vertical sides of the extended major cords and can be seen only by tilting the shell. This same type of "hidden" thread also occurs in *M. stueri*, which may indicate a close relationship.

Thus, the finding of the first fossil example of *Murexiella* s.s. in the Australian Tertiary, has raised more questions than it has answered. It has not shed any light on the ancestry of the *Subpterynotus* group or the problem of the disjunct distribution of the species presently referred to that group. Presumably both lines descended from an Eocene Tethyan ancestor but the intermediate stage in both lines remains as much of a mystery as it was ten years ago. The Eocene "*Murex*" *stueri* Cossmann seems the most likely ancestor for the Miocene Australian form. But for the Miocene *M. perculata* to evolve into the Pliocene *Subpterynotus antecedens* still requires considerable changes in morphology.

The development of the American side of the group is even less certain. There is not any Eocene species yet known that has any resemblance more than any other. The only species with which it can be associated are the European Aquitanian and Burdigalian "*Murex*" *subgranifer* Cossmann and Peyrot, 1923, which is virtually identical to the living "*Murex*" *exquisitus* Sowerby, 1904 (of unknown provenance), and the Helvetian and Tortonian "*Murex*" *graniferus* Michelotti, 1841. The Aquitanian "*M.*" *subgranifer* is certainly the ancestor of *Subpterynotus textilis* in the New World and *S. granifera* in the Old (it is very likely that these two latter species are synonymous) but, as yet, we have no candidate for any forerunner to *S. subgranifer*.

SYSTEMATIC DESCRIPTION

Family MURICIDAE da Costa, 1776

Subfamily MURICOPSINAE Radwin and D'Attilio, 1971

Genus MUREXIELLA Clench and Pérez Farfante, 1945

Murexiella CLENCH and PÉREZ FARFANTE, 1945: 49.

Type species: *Murex hidalgoi* Crosse, 1869, by original designation.

Minnimurex WOOLACOTT, 1957: 115.

Type species: *Minnimurex phantom* Woolacott, 1957, by original designation.

MUREXIELLA PERCULTA E.H. Vokes, sp. nov.

Plate 1, figs. 1-5

Description: Shell large for the group, spire low, body whorl inflated; five teleoconch whorls and a large, smooth, bulbous protoconch (number of whorls uncertain, invariably broken and plugged). Ornamentation initiated abruptly at a small varix; spiral ornamentation beginning with a single cord at periphery but by end of first post-nuclear whorl with three strong cords, these appearing on later whorls as high flat-topped flanges circling the shell; gradually smaller threads intercalated, two between the suture and shoulder cord and one between each pair of stronger cords; weak tertiary threads developed on the vertical, flattened sides of the major spiral cords, these numbering seven on the body whorl, plus an additional four or five on the siphonal canal, the latter also with secondary and tertiary threads intercalated; adult shell covered by alternating primary and secondary cords, tertiary threads not visible unless shell is tilted. Axial ornamentation on first post-nuclear whorl of about 12 laminae, lapping onto the smooth protoconch; strengthening into varices and reduced in number to about eight on the second post-nuclear whorl and ultimately to six or seven on the body whorl of the adult. Entire surface of shell covered with thin, axial growth lamellae, these becoming bunched together on both the ad- and abapertural faces of the varices; apertural face of varices covered by shingled laminae, looped over the spiral cords, giving the face an intricate filagree pattern; where spiral cords cross varices a series of square-bottomed grooves formed on adapertural side, crossed by the growth lamellae to form a row of square pits; terminal ends of the spiral cords strongly recurved but not extending past the lamellae. Aperture almost circular; columellar lip narrow, smooth; margin of outer lip crenulated into each of the spiral cords. Siphonal canal moderately long, slightly less than one-half total height of shell, wide, open by a narrow slit; distal end slightly recurved, terminations of previous canals forming a small umbilicus.

Holotype: National Museum of Victoria P 74075; height 34.4 mm, diameter 23.5 mm (Plate 1, fig. 1).

Paratype A: NMV P 74076; height 21.8 mm, diameter 16.1 mm (Plate 1, fig. 3).

Paratype B: NMV P 74077; height 23.5 mm, diameter 15.8 mm (Plate 1, fig. 4).

Paratype C: Australian Museum C.125233; height 24.0 mm, diameter 15.7 mm (Plate 1, fig. 2).

Paratype D: U.S. National Museum 375462; height 15.0 mm, diameter 10.4 mm (Plate 1, fig. 5).

Type locality: Fishing Point Marl, lower mollusk horizon (Longfordian), cliff 30 m above Lake Craven, Aire River. 0.5 km northwest of Red Hill, Horden Vale, Victoria.

Geological distribution of material studied:

BALCOMBIAN

Muddy Creek Marl:

USNM 375462 (paratype D), TU 1384, Muddy Creek, 8 kms west of Hamilton, Vic. (Coll. E.H. Vokes)

Fyansford Formation (=Balcombe Clay): Australian Mus. C.125233 (paratype C), Fossil Beach, Balcombe Bay, about 3 kms south of Mornington, Vic. (Coll. J. Kerslake and T.R. Garrard).

BATESFORDIAN

Fishing Point Marl, upper mollusk horizon.

NMV P 74084, top of cliff at Fischer's Point, 17m above Lake Craven, Aire River, Horden Vale, Vic.

LONGFORDIAN

Fishing Point Marl, lower mollusk horizon.

NMV P 74075 (Holotype) and P 74077 (paratype B), cliff 30 m above Lake Craven, Aire River, 0.5 km northwest of Red Hill, Horden Vale, Vic.

NMV P 74076 (paratype A), low cliff and dam, southeast of Fischer's Point, Lake Craven, Aire River, Horden Vale, Vic.

NMV P 74079 and 74080, cliff southeast of Fischer's Point, 10 m above Lake Craven, Aire River, Horden Vale, Vic.

(All NMV material coll. T.A. Darragh et al.)

Discussion: This elegant new species is based upon eight specimens, ranging in age from Longfordian to Balcombian (early to middle Miocene). Although obviously referable to the genus *Murexiella*, there is no other species with which it might be compared. As noted above, superficially it most nearly resembles the members of the genus *Homalocantha* but lacks the varical extension, or partition, above the aperture. It differs from the members of *Subpterynotus* in having much coarser ornamentation and in not having the varical flange as well developed, especially on the siphonal canal.

Most of the living species of *Murexiella* s.s. have about five major spiral cords on the body whorl. The Eocene species such as *M. stueri* and the American *M. mantelli* (Conrad, 1834) (see Vokes, 1968, pl. 5, fig. 1) have seven major cords, as does *M. perculata*, indicating that there has been a trend toward reduction in the modern species of *Murexiella*. In the American *S. textilis* there are still seven but in *S. tatei* there appear to be ten. However, of these, seven are slightly larger, suggesting that the other three arose as secondary threads, which ultimately became almost as large as the primaries. In the juvenile specimen of *M. perculata* (pl.1, fig. 5) this tendency can be seen, in that there are ten primary cords, all of almost equal strength. Can the development of the Australian members of *Subpterynotus* represent neoteny? Certainly there is a much greater degree of similarity between the juvenile example of *M. perculata* and *S. tatei* than there is with the adult specimens.

The name *perculata* (Latin- highly adorned) is in reference to the elaborate development of axial lamellae, which gives to this new species its strongest affinities with the subgenus *Subpterynotus*. Verco (1895, p. 84), in his original description of "*M*" *tatei*, made the observation that the surface of the shell had "an appearance of being covered with coral, or chain-stitch crochet work which is continuous over the varices." Although of a coarser design, the surface of *M. perculata* likewise has this dramatic decoration, especially on the varical faces.

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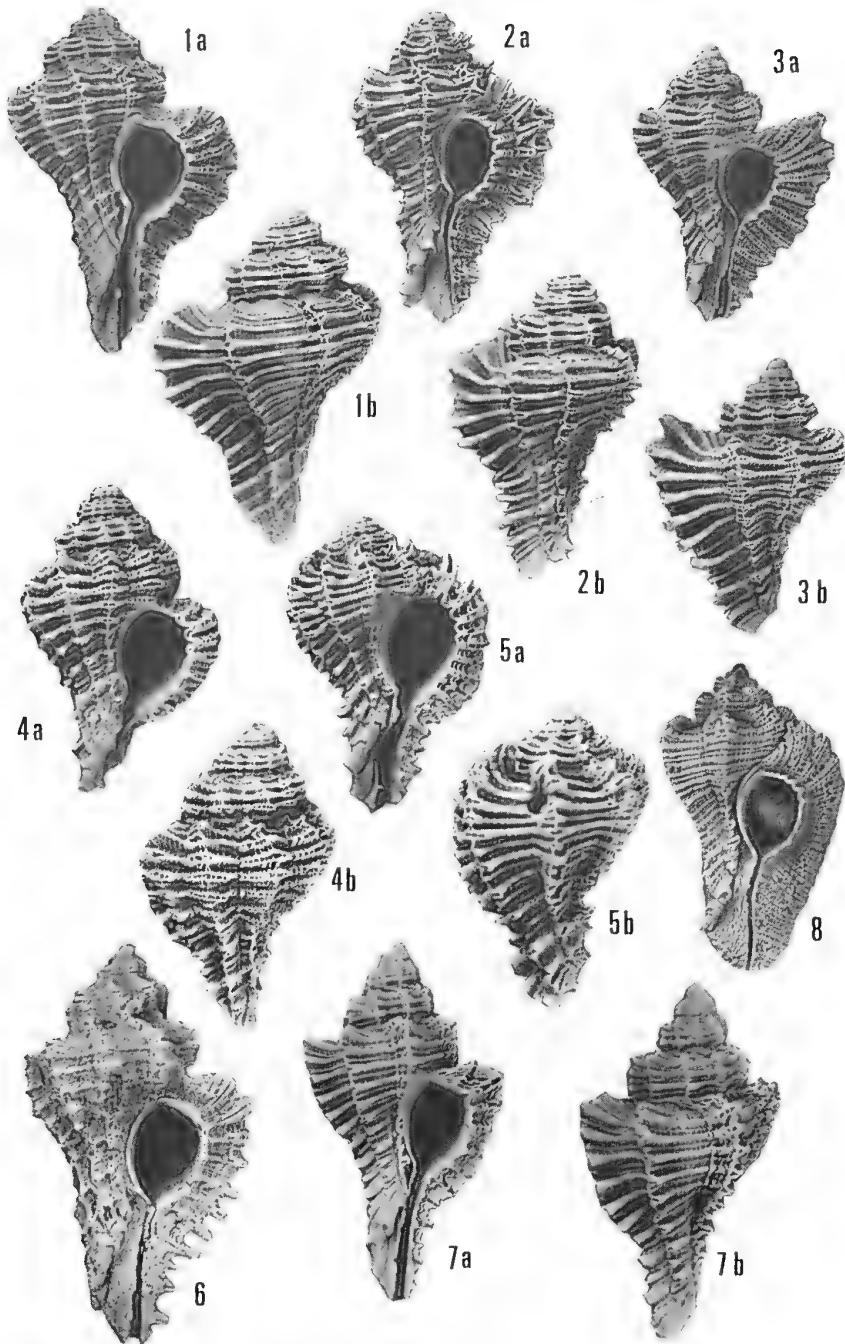
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PLATE 1

Figs.

- 1 - 5. *Murexiella perculata* E.H. Vokes, sp. nov.
 1. (X 1½) NMV P 74075 (holotype); height 34.4 mm, diameter 23.5 mm
Locality: Lake Craven, Horden Vale, Victoria.
 2. (X 2) Australian Museum C. 125233 (paratype C); height 24.0 mm, diameter 15.7 mm
Locality: Fossil Beach, Balcombe Bay, Victoria.
 3. (X 2) NMV P 74076 (paratype A); height 21.8 mm, diameter 16.1 mm
Locality: Lake Craven, Horden Vale, Victoria.
 4. (X 2) NMV P 74077 (paratype B); height 23.5 mm, diameter 15.8 mm
Locality: Lake Craven, Horden Vale, Victoria.
 5. (X 3) USNM 375462 (paratype D); height 15.0 mm, diameter 10.4 mm
Locality: TU 1384, Muddy Creek, Hamilton, Victoria.
6. *Murexiella crispangula* (Heilprin, 1887)
(X 1½) USNM 214442; height 42 mm, diameter 25 mm
Locality: Ballast Point, Tampa Bay, Florida, USA
7. *Murexiella stueri* (Cossmann, 1889)
(X 4) Nat. Hist. Mus. Basel H 17137; height 14.9 mm, diameter 8.5 mm
Locality: Chaussy, near Paris, France
8. *Murexiella (Subpterynotus) tatei* (Verco, 1895)
(X 2) Wright Coll; height 24.4 mm, diameter 14.3 mm
Locality: Smoky Bay, South Australia, 36 m ("20 fathoms")



The spawn and embryonic development of colour variants of *Dendrodoris nigra* Stimpson (Mollusca: Nudibranchia)

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ABSTRACT

Colour variants of *Dendrodoris nigra* from New South Wales produce morphologically different planktotrophic larvae. All colour variants deposit transparent gelatinous egg ribbons which are arranged spirally onto hard substrata. Embedded into the matrix of the ribbons are yellow zygotes. Colour variants which are brownish-black, gray or black with white speckles (form 1) can produce up to 251,000 zygotes (diameter 74-75 μm) per spawn. Form 1 embryos hatch 9.6 days after oviposition at 22-23°C. Newly liberated veligers (mean length 114 μm) are shaped like most planktotrophic opisthobranch larvae; each veliger has a transparent sinistrally coiled shell, operculum, hyperstrophically arranged visceral mass and a cephalopodal region which can be retracted into the shell. The subvelum of form 1 veligers is not well defined like that of form 2. Colour variants which are jet-black or black with red-rimmed mantles (form 2) produce up to 88,600 zygotes per spawn. Zygotes of jet-black variants (mean diameter 129 μm) are significantly larger ($P < 0.05$, Student's t-test) than those of variants with red-rimmed mantles (mean diameter 121 μm). Differences in diameter of zygotes have no effect on the shape of the veligers. Form 2 embryos hatch 9.2 days after oviposition at 22-23°C. Mean shell length of newly liberated veligers produced by jet-black variants is 153 μm , 9 μm greater than that of veligers produced by variants with red-rimmed mantles. Compared to most planktotrophic opisthobranch larvae, the shape of form 2 veligers is atypical in that each lacks an operculum and possesses an oversized cephalopodal region which can not be retracted into the shell. The shell of form 2 is darkly pigmented when embryos are reared in the laboratory. Colour variants do not appear to vary their developmental mode and in the laboratory copulation occurs only between individuals with the same colour pattern. Differences in larval morphology suggests that certain colour variants of *D. nigra* may be separate (sibling) species.

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INTRODUCTION

Dendrodoris nigra Stimpson, 1856 is a sponge-eating (Bloom, 1976), Indo-Pacific nudibranch found along the east and west coasts of Australia (Allan, 1947; Thompson, 1975; Roberts & Wells, 1980). Adults of this species from east Africa and India are known to vary in colour, texture of the mantle and in number of branchiae (Gohar & Soliman, 1967; Narayanan, 1968). Specimens from New South Wales also display variations in colour that are comparable to those recorded from other regions of Australia (Allan, 1947; Burn, 1969), Hawaii (Kay & Young, 1969), Egypt (Gohar & Soliman, 1967) and Tanzania (Edmunds, 1971). As in Hawaii (Kay & Young, 1969), colour variants of *D. nigra* from New South Wales produce planktotrophic larvae which hatch from egg-mass ribbons deposited on hard substrata. The shape of the spawn and patterns of embryogenesis, however, differ for certain colour morphs.

In this paper the egg masses and larval development of several colour variants of *D. nigra* from New South Wales are described for the first time and compared with those of its congeners. Discrepancies in spawn and embryogenesis suggest that separate (sibling) species might exist.

MATERIALS & METHODS

All nudibranchs collected matched the descriptions recorded for *D. nigra* by Allan (1947) and Thompson (1975). Specimens taken intertidally at Long Reef, Sydney during 1976 to 1979 were either black with white-speckled dorsal surfaces, gray or brownish-black (Table 1). Specimens taken intertidally at Pilot Beach, Laurieton during 1979 were jet-black with the inside edge of the mantle skirt outlined in red and specimens collected intertidally at Bottle & Glass, Sydney and subtidally at Clovelly, Sydney during 1979 were jet-black (Table 1).

Animals were brought back to the laboratory and kept in aquaria. Egg masses produced in the laboratory or collected in the field were placed in glass bowls filled with filtered seawater at 22–23° and 33–34‰S. Larvae were fed unicellular phytoplankton (*Pavlova lutheri*, *Isochrysis galbana* and *Phaeodactylum tricornutum*) but failed to grow and died after ten days.

Observations on developmental patterns of each colour variant were made with a phase contrast microscope. Photographs were taken with a camera and flash unit attached to the microscope. Morphometric characteristics of the zygotes, capsules and veligers of different colour variants were analyzed with either a paired Student's t-test or balanced one-factor analysis of variance (ANOVA). Significant differences between colour variants were further tested a posteriori with a Student-Newman-Keuls (SNK) multiple comparison test (Sokal & Rohlf, 1969).

Nudibranchs which were black and speckled, gray or brownish-black always produced identical spawn and embryos, and will be referred to as *D. nigra* (form 1). Except for differences in the sizes of the spawn and eggs, colour morphs which were jet-black or red along the edge of the mantle produced identical embryos, and will be referred to as *D. nigra* (form 2).

RESULTS

Spawn

In the laboratory copulation occurs only between specimens with the same colour pattern. Egg masses produced by both forms are Type A (as defined by Hurt, 1967) or a₁ (as defined by Fernandez-Ovies, 1981) and are similar to those recorded for *Dendrodoris gemmacea* by Baba (1956) and Rose (1981) and *D. fumata* by Gohar & Soliman (1967). Except for nudibranchs with red-rimmed mantles, all other colour morphs deposit spirally coiled, transparent ribbons with double-membraned egg capsules unevenly packed two or three layers deep within the gelatinous matrix of each ribbon. Egg masses produced in the laboratory by these nudibranchs are identical to those collected in the field.

Only one egg mass produced by nudibranchs with red-rimmed mantles was observed. The ribbon was similar to the others except that it was smaller and deposited in a semi-circular rather than spiral pattern. Whether this semi-circular configuration is typical or the result of the laboratory conditions was not determined.

Each egg capsule generally encases one yellow or brownish-yellow zygote but form 1 egg ribbons can contain anything up to 11 zygotes per capsule. Capsules encasing more than two zygotes are tubular, enclosing a single row of zygotes and oriented vertically with respect to the attached edge of the ribbon (Plate 1, A). Form 1 egg ribbons are more flaccid than those of form 2 and often have as many as three grooves running lengthwise along the ribbon. These grooves caused by uneven spacing of capsules within the ribbon matrix, occur when a monolayer of capsules is present or when gaps exist within the layers of capsules.

For both forms 1 and 2, the total number of zygotes contained within an egg ribbon varies with the length of ribbon. The mean number per ribbon produced by form 1 is generally three or four times greater than that produced by form 2 (Table 1). Under laboratory conditions, a 220 mm long ribbon deposited by a white-speckled *D. nigra* (form 1) will contain up to 242,850 zygotes while a 120 mm long ribbon deposited by a jet-black *D. nigra* (form 2) will contain 67,584. The total number of zygotes produced by nudibranchs with red-rimmed mantles was not calculated but it is estimated to be tens of thousands for spawn ranging from 60 to 70 mm in length.

Mean diameters of the zygotes and capsules of form 1 colour morphs, form 2 (red-rimmed mantle) and form 2 (jet-black) are as follows: 74-75 and 121-122 μm ; 121 and 140 μm ; and 129 and 163 μm , respectively (Table 1). Zygotes produced by nudibranchs with red-rimmed mantles are significantly smaller than those belonging to jet-black specimens (t-test: $t=5.25 > t_{0.05}=2.038$; $P<0.05$). However, they are significantly larger than those belonging to form 1 colour morphs (t-test: $t=6.896 > t_{0.05}=2.548$; $P<0.05$). The capsule size of the zygotes of different colour morphs are significantly different (one-factor ANOVA: $F_4, 45=5.04$; $P<0.01$). A SNK test indicates that the mean sizes of form 1 and form 2 (red-rimmed mantle) are not significantly different from each other ($P>0.05$) but that they are all significantly smaller ($P<0.05$) than capsules produced by form 2 (jet-black).

Development

For either form, there is no difference in the development of embryos from egg masses laid in the laboratory or collected from the field. Embryos of forms 1 and 2 take between 9 and 9.6 days to hatch when incubated at 22-23°C (Table 1). The timing of different stages of development are listed in Table 2. Photographs of a number of these stages are shown in Plates 1 and 2.

Early development to trochophore (Plate 1, A to D)

Except for differences in the size of zygotes, early development up to the trochophore stage or embryogenesis in embryos of either colour form is similar and comparable to that described for other nudibranchs (e.g., Casteel, 1904; Thompson, 1976; Rose, 1981). Briefly, first and second cleavage are equal, holoblastic and meridional (Plate 1, A and B). Cleavage beyond the two cell stage is spiral and at the eight cell stage formation of the first set of micromeres is asynchronous (Plate 1, B). The micromeres at this stage are displaced dextrorotically with respect to their blastomeres. During the blastula stage embryos are flattened dorso-ventrally. By the second day after oviposition they are at gastrula.

The process of gastrulation is a mixture of invagination and epiboly, resulting in a ventrally positioned blastoporal cleft along the sagittal plane of the embryo. At this stage form 1 and 2 embryos appear heart-shaped (Plate 1, C and D). Gradually the cleft disappears except antero-ventrally where it forms a circular depression of lightly coloured cells (the blastopore), marking the future site of the stomodoeum. Towards the end of gastrulation, the anal cells on a number of form 2 embryos can be seen postero-ventrally and to the left of the sagittal plane; anal cells are not observed on form 1 embryos at this stage.

The morphology of form 1 and 2 embryos begins to differ at the trochophore stage. Although both forms develop a slow arrhythmically beating prototroch and a shell gland, form 1 embryos still fail to display a pair of anal cells or a thin protruding rudimentary metapodium like that observed in form 2.

Early, middle and late veliger stages (Plate 1, E and F; Plate 2, A and B)

The first signs of bodily movement occur at the early veliger stage for embryos of both forms. Although shaped differently, form 1 and 2 embryos at this stage possess a stomodoeum, rudimentary velum and metapodium and a pair of anal cells, situated mid-ventrally just beneath the metapodial rudiment. Their visceral mass is still undifferentiated and opaque from large amounts of yolk. When viewed laterally, the shell gland of embryos of both forms is positioned mid-dorsally and can be seen as a long slightly raised mound of translucent cells.

Form 1 embryos at the early veliger stage display a darkly pigmented mass of cells which is located posteriorly on the left side, just beneath the surface of the body (Plate 1, E). Whether this pigmented mass of cells is the secondary (embryonic) kidney as described in other opisthobranchs (Thompson, 1958; Bridges, 1975; Bonar, 1978) was not determined. However, during the later stages of development the mass moves to the right side, beneath the anus and develops either into two large empty cells or remains darkly pigmented. Form 2 embryos at this stage typically have polar bodies adhering to the outer edges of their stomodoeum which consists of a deep depression of semi-transparent cells (Plate 1, F).

Form 1 and 2 embryos begin rotating during the middle veliger and at this stage their mantle and shell have advanced enough to completely enclose the visceral mass. Form 1 embryos at the beginning of the middle veliger stage have no mantle cavity, statocysts or pedal glands but like form 2, the anal cells towards the end of this stage have reached their definitive position ventrolaterally on the surface of the right side of the embryo. The rudimentary velum of form 2 becomes bilobed at this stage and the metapodium develops two statocysts. This does not occur in form 1 until the late veliger stage.

Towards the end of the middle veliger stage the visceral mass of form 2 embryos differentiates into an alimentary tract. The oesophagus is short and straight and attached to the stomach anterodorsally. The stomach is opaque and partially obscured from view by the digestive diverticula and a large translucent vesicle located posteriorly on the left side of the embryo, between the left digestive diverticulum and stomach. In form 1 embryos, a translucent vesicle of this kind is not observed. Although both digestive diverticula of form 2 are still filled with yolk at the middle veliger stage, the left is twice as large as the right. The hindgut is a dark narrow tube which is slightly wider at the beginning where it leaves the stomach postero-dorsally. It loops over the dorsal region of the embryo to the right side and traverses over the top of the secondary (embryonic) kidney until it opens into the mantle cavity through the anus, near the two anal cells. The secondary kidney of form 2 embryos at the middle veliger stage appears as a large, dark mass of cells located in the right dorso-lateral region of the embryo, at the base of the velum. As in *D. fumata*, it is a large oval structure and is multicellular in composition (Gohar & Soliman, 1967). The final fate of the secondary kidney was not determined because unfortunately the shells of form 2 embryos become too opaque for external observations beyond the middle veliger stage. The nephrocysts could not be found but they are probably adjacent to and left of the secondary kidney, as described for *D. fumata* by Gohar & Soliman (1967).

The transition between the middle and late veliger stages is more subtle in form 2 embryos than in form 1 as their visceral mass has already become fully differentiated by the end of the middle veliger stage. Moreover, as stated above, detection of the late veliger stage in form 2 is confounded by the intense pigmentation of the shell which prevents viewing of the final position and state of the visceral organs. According to Gohar & Soliman (1967), the degree of opaqueness of the larval shell of *D. fumata* is directly related to the intensity of light to which embryos are exposed. Whether or not this is the case with *D. nigra* (form 2) was not tested. Larval shells of *D. nigra* (form 1) do not become pigmented.

Morphogenesis of the cephalopodal region is the only event distinguishing the late veliger stage from the middle veliger in form 2 embryos. During the late veliger stage, velar lobes of form 2 embryos grow larger and develop well-defined subvela (Plate 2, B and D). Unlike form 1, the cephalopodal region becomes so large that the embryos are unable to retract into their shells. Their transparent velar lobes are composed of large refringent granules and are provided, along the outside edge, with a broad margin of cells supporting locomotory cilia. The subvelum is a thick ridge of refringent granules covered with short cilia which are in line with and connected to the mouth. Unlike form 1, the metapodium (foot) of form 2 does not possess an operculum and is extremely broad and long, curving around the posterior portion of the shell (Plate 2, B). The foot is granular like the velum and the edge of the sole is fringed with a thick row of these granules; embedded into the tissues at the proximal end is a pair of statocysts.

Although considerably smaller than form 2, form 1 embryos at the late veliger stage also have a fully developed cephalopodal region. The mantle fold which has separated from the lip of the shell allows the embryos to retract into their shells. A columnar (or retractor) muscle is visible as a translucent, fibrous strand positioned on the left side of the embryo. The muscle is inserted into the neck of the left velar lobe and attached to the inside wall of the shell on the left posterior side of the embryo. The bilobed velum of form 1 embryos is thick and each lobe consists of a single row of large refracting marginal cells connected to the head region by epithelial tissue. Like form 2, the marginal cells of form 1 support a dense array of locomotory cilia. Unlike form 2, however, the subvelum is poorly defined with a sparsely ciliated feeding groove on the outside wall of each velar lobe, below the preoral band of ciliated marginal cells. The metapodium is narrow and embedded in the tissue, at the proximal end, is a pair of statocysts. At the distal end of the metapodium, there is a cluster of translucent pedal glands. The sole of the metapodium is covered with short cilia and the upper surface has a transparent operculum attached to it.

Alimentary tract of form 1 embryos at the late veliger stage is similar to that described above for form 2 embryos at the middle veliger stage. Differences do occur in the shape of various organs. The stomach of form 1 is at least twice as large as the digestive diverticula and is kidney-shaped. Like form 2 embryos, the semi-transparent wall of the stomach is composed of refringent granules and the lumen is ciliated. The left digestive diverticulum in form 1 at this stage is more opaque than the right, but is scarcely larger than the right. A pair of translucent cells, which may be the nephrocysts or secondary kidney, is located in the neck of the cephalopodal region, antero-dorsal to the anus. The entire visceral mass of embryos of both forms at the late veliger stage is enclosed in a perivisceral membrane which separates it from the shell.

Veligers (Plate 2, C and D)

Typical of planktotrophic larvae (Type 1, as defined by Thompson, 1967), the newly hatched veliger larvae of both forms lack eye spots and a propodium. They are positively phototactic and their type 1 shells (as defined by Thompson, 1961) are sinistrally coiled while their asymmetrical bodies are dextrally or hyperstrophically arranged. The shells of form 1 veligers are transparent while those of form 2 are heavily pigmented (Plate 2, C and D).

Mean shell lengths of form 1, form 2 (red-rimmed mantle) and form 2 (jet-black) are as follows: 114 μm , 144 μm , and 153 μm , respectively (Table 1). These shell lengths are significantly different to each other (one-factor ANOVA: $F_{4,45}=114.7$; $P<0.001$). A SNK test indicates that the mean lengths of all form 1 colour morphs are equivalent to each other ($P>0.05$) and less than that of form 2 (red-rimmed mantle) ($P<0.05$), which in turn, is less than that of form 2 (jet-black) ($P<0.05$).

The cephalopodal region of form 2 veligers is at least three times larger than that of form 1. The mean distance between the outside edges of a fully extended velum of form 2 (jet-black variant) is 267 μm (S.D. $\pm 12 \mu\text{m}$, $n = 5$). This distance is greater than that found for veligers of *Dendrodoris fumata*, which is 225 μm (Gohar & Soliman 1967).

DISCUSSION

Compared to other *Dendrodoris* species (Table 3), *D. nigra* (form 1) produces high numbers of small planktotrophic eggs per spawn. *D. nigra* (form 2) also produces high numbers of planktotrophic eggs but they are the third largest in diameter. The overall appearance of form 1 veligers is more like that of *D. gemmacea* than like that of form 2. The dark pigmentation of the shell and shape of the cephalopodal region of form 2 veligers are similar to that of *D. fumata*, however, unlike this species, the cephalopodal region of form 2 is much larger, lacks an operculum and is too large to be fully retracted into the shell. In this respect form 2 veligers are similar to the planktotrophic veligers of *Aegires punctilucens* described by Thiriot-Quievreux (1977), except that the cephalopodal region of this species is larger than that of form 2.

Different larval forms produced by colour variants of *Dendrodoris nigra* may indicate that this species is capable of some degree of developmental variability (poecilogony) rather than consisting of two separate species. Widespread species, such as *D. nigra* can have varying developmental patterns associated with different areas of their geographic range. According to Clark & Goetzfried (1978), several sacoglossans and nudibranchs have been shown to have variable development either between or within populations. Eyster (1979) has demonstrated that development within the same population of the aeolid *Tenellia pallida* from South Carolina could be either planktotrophic or non-pelagic (veligers metamorphose inside their capsules before hatching). Clark *et al.* (1979) have shown that development within the same population of the sacoglossan *Elysia cauze* from Florida can vary seasonally, with planktotrophic, lecithotrophic and direct (non-pelagic) development occurring in sequence. West *et al.* (1984) have reported that separate populations of *E. chlorotica* are able to produce either planktotrophic or direct developing larvae.

Cases cited above by these authors, however, involve opisthobranchs which change from one mode of development to another. This does not appear to happen in *Dendrodoris nigra*. Instead, two forms of the same developmental mode are produced. Why should the same species produce two morphologically different larvae that fulfil the same ecological function (i.e., dispersal of offspring)? Adults of *D. nigra* (forms 1 and 2) do not exhibit self-fertilisation like that reported for *Cuthona adyarensis* by Rao (1961). Nor do they change their developmental mode as a result of starvation in the adult like that observed with *Spurilla neapolitana* (Clark & Goetzfried, 1978). Furthermore, neither the size of the adults nor certain extrinsic factors (such as temperature and salinity) could be shown to alter the developmental mode of *D. nigra* from planktotrophy to any of the other modes (Rose, 1981). Consequently, none of the above factors can account for the two larval forms found in different colour variants of *D. nigra*.

According to Eyster & Stancyk (1981) one of the main environmental factors influencing the growth, size and fecundity of the sponge-eating dorid, *Doriopsilla pharpa*, appears to be the abundance of food. Similarly, differences in the egg diameter and number of eggs per spawn found between forms 1 and 2 may be due to differences in the type and amount of food (sponge) associated with the habitat of each colour variant. Differences in larval morphology between forms 1 and 2 suggest that the two forms are adapted for different life cycles. The enlarged velum of form 2 veligers indicates that they may be better suited for longer planktonic periods, or that they may be specialised feeders and stronger swimmers. The transparent larval shells of form 1 and pigmented shells of form 2 may reflect adaptations to different microhabitats by each colour variant of *Dendrodoris nigra*.

Forms 1 and 2 may be sibling species which are sympatric in New South Wales. The lack of observed evidence of copulation in the laboratory between specimen with different developmental patterns and differences between the structure of their spawn, morphology of their larvae and colour of the adults may reflect early stages of speciation. Observed evidence that form 2 veligers are unable to retract into their shell and have a permanently extended, oversized foot without an operculum suggests that forms 1 and 2 have started diverging. According to Gallardo (1977) a similar process is occurring in the prosobranch *Crepidula dilatata* from southern Chile. For this species subtle differences exist in: adult colouration; shape of the egg capsules; egg diameters; spawning seasons; abundance and distribution of adults in the intertidal zone; and differences in developmental types (planktotrophy and direct) (Gallardo, 1977).

Embryological discrepancies and lack of evidence of copulation between specimens with different developmental patterns, suggest that some of the colour variants presently considered *Dendrodoris nigra* might be sibling species. Before separating these colour variants into different species, however, it will first be necessary to examine in detail the internal morphology of the adults of various colour morphs (especially the reproductive anatomy) and their ecology (habitats, food and reproductive cycle).

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TABLE 1. Collection data and developmental characteristics of *Dendrodoris nigra* (forms 1 & 2). Numerical data are presented as mean \pm SD with sample size in brackets. Days to hatching are derived from various egg masses incubated at 22-23°C. Number of egg masses used are shown in brackets.

Development Form		Season Collected			Year(s)	Length of Field-collected Animals (mm)	Number of Egg Masses		Eggs/Spawn	Dia. of Eggs (μ m)	Dia. of Capsules (μ m)	Shell Length at Hatching (μ m)	Days to Hatching
Colour morph	Locality	Su	Au	Sp			Field	Laboratory					
FORM 1													
WHITE-SPECKLED	LONG REEF	x	x	x	1976 1977 1978 1979	54.4 \pm 9.9 (8)	4	16	242 000 \pm 8 799 (5)	74.6 \pm 1.3 (10)	121.4 \pm 7.4 (10)	114.2 \pm 7.8 (10)	9.6 \pm 0.6 (4)
BROWN-BLACK	LONG REEF	x	x	x	1976 1977 1978 1979	57 \pm 12 (5)	2	5	240 266 \pm 10 000 (4)	73.5 \pm 1.6 (10)	121.2 \pm 6.1 (10)	113.9 \pm 6.2 (10)	9.4 \pm 0.2 (2)
GRAY	LONG REEF	x			1979	61 \pm 2 (3)	1	1	234 100 (1)	74.3 \pm 1.6 (10)	121.6 \pm 6.3 (10)	114 \pm 6.6 (10)	9.0 (1)
FORM 2													
JET-BLACK	BOTTLE & GLASS CLOVELLY	x	x	x	1979	65.7 \pm 4 (3)	1	5	67 584 \pm 21 000 (3)	129 \pm 3.0 (20)	162.5 \pm 5.0 (10)	152.8 \pm 3.1 (10)	9.2 \pm 0.7 (2)
RED-RIMMED MANTLE	PILOTS BEACH	x			1979	34 \pm 1 (3)	0	1	tens of thousands	121.4 \pm 8.1 (43)	140.3 \pm 7.1 (10)	144 \pm 2.7 (10)	9.3 (1)

TABLE 2: *Dendrodois nigra* (form 1 & 2). Chronology of developmental stages from oviposition to hatching for 50% or more embryos from several egg masses when incubated at 22-23°C. Times are shown as mean \pm SD with number of egg masses in brackets.

DEVELOPMENTAL STAGE	TIME	
	FORM 1	FORM 2
Oviposition	0	0
Expulsion of 2nd polar body	2.6 \pm 0.5 (3)	2.8 \pm 0.4 (2)
First cleavage	3.3 \pm 0.3 (4)	5.5 \pm 0.4 (2)
Second cleavage	5.5 \pm 0.6 (4)	9.8 \pm 0.5 (2)
Third cleavage	13.0 \pm 1.2 (4)	12.3 \pm 0.9 (2)
Fourth cleavage	15.3 \pm 1.5 (4)	17.0 \pm 1.6 (2)
Morula	22.0 \pm 1.0 (3)	20.0 \pm 1.4 (2)
Blastula	1.2 \pm 0.1 (7)	1.0 \pm 0.5 (3)
Gastrula	2.2 \pm 0.3 (7)	2.2 \pm 0.5 (3)
Trochophore	4.1 \pm 0.1 (3)	4.1 \pm 0.7 (3)
Early veliger	5.1 \pm 0.7 (4)	4.1 \pm 0.3 (3)
Middle veliger	5.8 \pm 0.4 (4)	5.8 \pm 0.6 (3)
Late veliger	7.7 \pm 0.5 (4)	7.4 \pm 0.2 (3)
Hatching	9.6 \pm 0.6 (4)	9.2 \pm 0.7 (3)

TABLE 3: The body length, number of eggs per egg mass, egg diameter and developmental type of species of *Dendrodroris* from various parts of the world. Dash indicates no data.

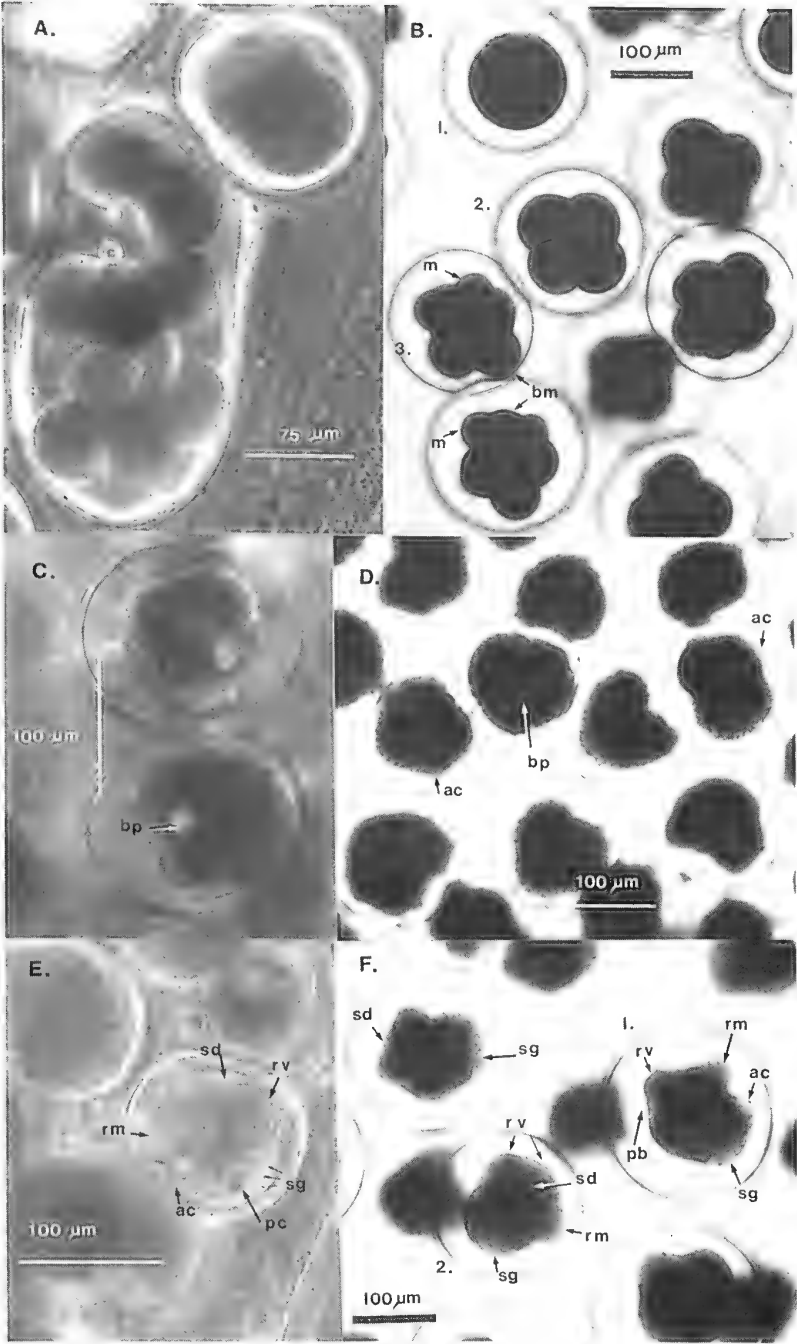
Species	Length (mm)	Eggs per egg mass	Egg dia. (μ m)	Dev. type	Reference
<i>Dendrodroris denisoni</i> (Angas)	35-60	2 664	186	direct (non-pelagic)	Rose (1981)
<i>D. fumata</i> (Rüppell & Leuckart)	55	3 344 165 490	100	planktotrophic	Gohar & Soliman (1967)
<i>D. gemmacea</i> Alder & Hancock	60-70	10 000	105	planktotrophic	Rose (1981)
<i>D. krebsii</i> (Mörch)	— —	10 500 —	205 —	direct planktotrophic	Clark & Goetzfried (1978) Bandel (cited by Clark & Goetzfried (1978))
<i>D. nigra</i> (Stimpson)					
form 1	45-70	230 000 251 000	75	planktotrophic	present study
form 2	33-68	46 584 88 600	121-129	planktotrophic	present study

KEY TO LETTERING

anus (a); anal cells (ac); blastomere (bm); blastopore (bp); hindgut loop (hg); larval retractor muscle (lm); left digestive diverticulum (ld); locomotory cilia (lc); metapodium (mp); micromere (m); mouth (mo); operculum (op); pigmented mass of cells (pc); polar body (pb); right digestive diverticulum (rd); rudimentary metapodium (rm); rudimentary velum (rv); shell (sh); shell gland (sg); stomodoeum (sd); statocysts (s); stomach (st); subvelum (sv); velum (v).

PLATE 1

Dendrodoris nigra. A. Form 1 (white-speckled colour variant) : lateral view of embryos at two- and four-cell stage 8 hr after oviposition; note tubular capsule. B. Form 2 (jet-black colour variant) : unfertilised ovum (1.), four-cell stage (2.), and eight-cell stage (3.), 14 hr after oviposition. C. Form 1 (white-speckled) : 2.2 day-old gastrulae with blastopores seen as circular depressions of lightly coloured cells. D. Form 2 (red-rimmed colour variant) : 2.2 day-old gastrulae, note anal cells. E. Form 1 (white-speckled) : left-lateral view of 5.1 day-old early veliger; note darkly pigmented mass of cells. F. Form 2 (jet-black) : right-lateral view (1.) and right-ventro-lateral view (2.) of 5.1 day-old early veligers; note polar body adhering to surface of stomodoeum.



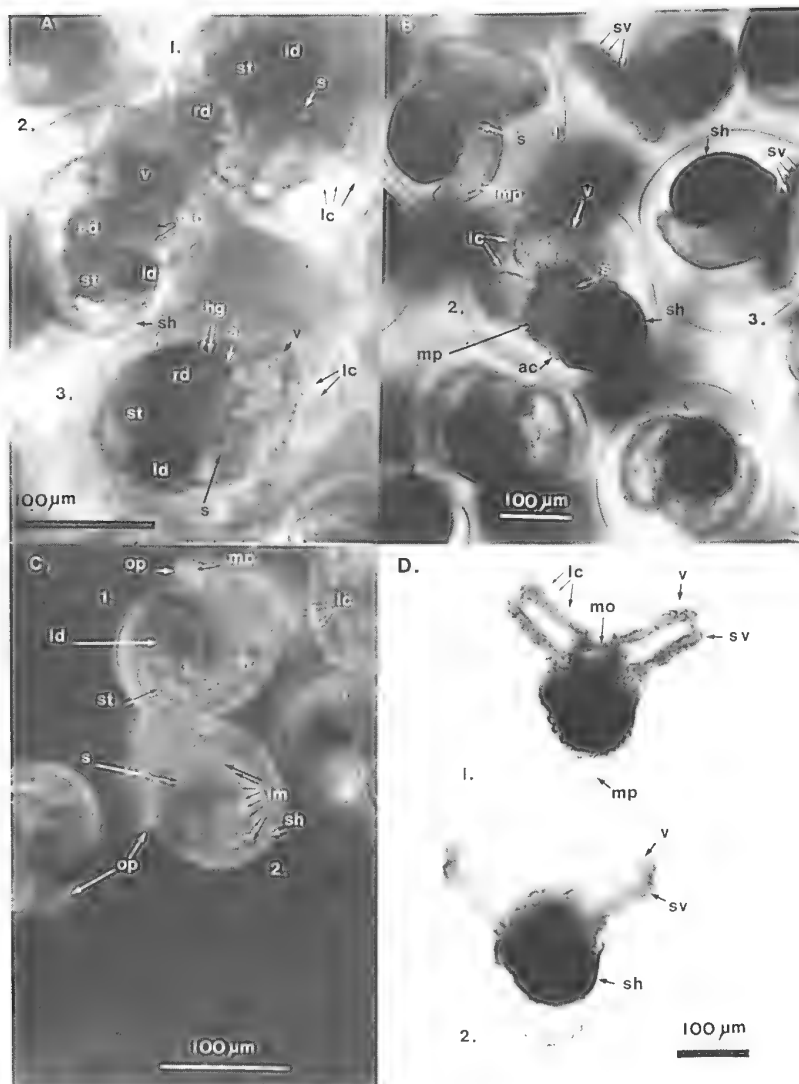


PLATE 2

Dendrodoris nigra. A. Form 1 (white-speckled colour variant) : left-lateral view (1.), right-ventro-lateral view (2.) and ventral view (3.) of 7.3 day-old embryos at late veliger. B. Form 2 (jet-black colour variant) : right-lateral view (1.), postero-ventral view (2.) and right-lateral view (3.) of 7.4 day-old embryos at late veliger. C. Form 1 (white-speckled) : left-ventro-lateral view (1.) and left-lateral view (2.) of newly hatched veligers 9.6 days after oviposition. D. Form 2 (jet-black) : ventral view (1.) and dorsal view (2.) of newly hatched veligers 9.2 days after oviposition.

Description of two new muricean species (Gastropoda: Muricidae) from Sri Lanka and Western Australia

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ABSTRACT

Two new species of the family Muricidae are named. *Orania alexanderi*, included in the subfamily Ergalataxinae, is described from Trincomalee, Sri Lanka. *Typhis (Typhis) wellsii*, a member of the subfamily Typhinae, is described from north of Port Hedland, Western Australia.

INTRODUCTION

The muricid subfamily Ergalataxinae is being studied by Dr Emily H. Vokes (Tulane University) and her help was most useful to include the new species described here in an adequate genus. After revision, this obscure subfamily will include many species (and genera) previously included in the Muricinae, Muricopsinae and Trophoninae.

The better known subfamily Typhinae includes several Australasian species, both fossil and recent. The new taxon is here compared with two recent and five fossil species.

TAXONOMY

Subfamily: Ergalataxinae Kuroda, Habe & Oyama, 1971.

Genus: *Orania* Pallary, 1900

Type species: *Murex spadae* Libassi, 1859 by O.D. (= *Murex fusulus* Brocchi).

***Orania alexanderi* R. Houart sp. nov.**

Plate 1, figures 1-4.

Description

Shell moderately large for the genus, maximum length 20 mm. Color dark orange to dark brown, with brown specimens showing orange-coloured spiral cords.

Aperture ovate, elongate, light purple. Columellar lip completely adherent to the shell or very slightly erect on 2/3 of its anterior part; it bears 3 to 4 small denticles posteriorly and a shallow

callus posteriorly. Outer lip slightly crenulate; inner side bearing six strong elongate, lighter-coloured denticles. Anal sulcus deep, well delimited by a moderately strong callus on its left and by a denticle on its right; slightly channelled posteriorly. Spire high, consisting of $3\frac{1}{2}$ polished, conical nuclear whorls and 6 to 7 postnuclear whorls. Suture impressed.

Body whorl bearing 7 to 8 moderately strong axial ridges; no other axial sculpture. Spiral sculpture consisting of 5 squamous cords and fine intermediate squamous threads. Usually lighter-coloured nodes are formed where the cords cross the axial ridges. Four to 5 threads on the shoulder and a large cord just below the suture, also appearing on the earlier whorls. One squamous cord on the siphonal canal.

Siphonal canal short, open, very slightly backward bent.

Type material

Holotype and one paratype in the Institut Royal des Sciences Naturelles de Belgique in Brussels. IRSNB No. 26811/1 and 26811/2.

1 paratype in the Museum National d'Histoire Naturelle, Paris, type collection.

1 paratype British Museum (Natural History) No. 1984161.

1 paratype Natal Museum, S. Africa, No. J8581/T2963.

1 paratype Australian Museum, Sydney, No. C143672.

2 paratypes Natural Museum of Sri Lanka.

All specimens ex R. Isaacs collection.

Type locality

Trincomalee, Sri Lanka, taken by fishermen.

Etymology

Named after Mr Brian Alexander from Sri Lanka, who kindly sent some lots of this shell for examination.

Discussion

The genus *Orania* is here chosen for the affinities between the radula of *Orania alexanderi* and that of the type species. Moreover, the dentate aperture, the multispiral protoconch and the general outline of the shell demonstrate the relationship with that genus, within the subfamily. This new species is very different from any other species belonging to this subfamily and no species other than *Murex infans* E.A. Smith, 1884 (*Muricopsis infans* of authors) could be reasonably compared. *M. infans*, the holotype of which was illustrated by Kaicher (1980), is smaller, has a broader aperture, fewer spiral cords and lacks the spiral cord on the shoulder. Another species, *Murex singaporensis* A. Adams, 1853, which could be in the Ergalataxinae, could not be compared as it was never illustrated, and there is no trace of a type in the BM(NH), where the A. Adams types are deposited; this species may be regarded as a *nomen dubium*.

Subfamily: Typhinae Cossmann, 1903

Genus: *Typhis* Montfort, 1810

Type species: *Purpura tubifer* Bruguière, 1791, by O.D.

***Typhis (Typhis) welshi* sp. nov.**

Plate 2, figures 1-3.

Description

Shell medium sized for the genus, broadly fusiform; greyish-white or pinkish-white on its whole surface. Aperture of the same color, small, rounded, forming an entire, erect and smooth peristome; no apparent anal notch.

Spire high, consisting of $1\frac{1}{4}$ to 2 glossy, large and rounded nuclear whorls and 5 large, rounded postnuclear whorls. Suture slightly appressed. Body whorl bearing 4 rounded varices, joining the preceding whorl with a strong varical buttress. Varices ornamented with 4 closed, slightly upwardly recurved spines. Carinal spine longest.

One white anal tube present between each varix, rising from the succeeding varix, strongly backward recurved and a little upward.

Spiral sculpture of the body whorl consisting of 4 to 6 very shallow cords. Siphonal canal moderate in length, acute, completely sealed, slightly bent to the right and bearing a short, backward recurved sharp and closed spine on its base.

Type material

Holotype No. 3076-83 in the Western Australian Museum.

Type locality

114 nautical miles north of Port Hedland, Western Australia, Stn. 5, 02/82/13A, L. Marsh on "Soela", 2. iv. 1982, dredged 201 m, limestone rubble and gray mud.

Dimensions

Holotype: 22 x 14.5 mm.

Etymology

Named after Dr F.E. Wells, Head of the Department of Malacology of the Western Australian Museum, who originally illustrated the shell in "Australian Shell News" and who kindly sent it to me for study.

Discussion

Typhis wellsii was previously illustrated in Australian Shell News (Wells, 1983) under the name *Typhina philippensis*. The originally illustrated specimen is here made the holotype.

It may be compared with seven more or less related species discussed by Vella (1961). From *T. philippensis* Watson, 1883 and *T. philippensis interpres* Iredale, 1924 it differs by its broader and larger protoconch; both, species and subspecies, are missing also the typical varical buttress of *T. wellsii* and have larger apertures. From *T. maccoyi* Tenison Woods, 1876, an Oligocene fossil of Tasmania, it differs by its smaller aperture, larger protoconch and the presence of the varical buttress; *T. maccoyi* has also a more slender siphonal canal. *T. planus* Vella, 1961, *T. hebetatus* Hutton, 1877, *T. adventus* Vella, 1961 and *T. clifdenensis* Vella, 1961 Oligocene and Miocene fossils of New Zealand differ all by missing the very typical varical buttress. Moreover, *T. hebetatus* has almost horizontal and larger tubes and a larger aperture. *T. adventus*, the most similar species, has sharper varices and a more ovate aperture.

ACKNOWLEDGEMENTS

I am most grateful to Dr F. Wells (Western Australian Museum) and to Mr Ralph Isaacs (London) who gave me the opportunity to examine these species; to Dr P. Bouchet (Museum National d'Histoire Naturelle, Paris) for the most useful scanning micrographs of the radula and to Dr P.A. Maxwell (New Zealand Geological Survey) who procured and loaned me fossil species for comparison. Thanks also to Dr W.F. Ponder and Mr I. Loch (Australian Museum, Sydney) for the loan of *Typhis philippensis interpres* (holotype); to Mr B. Marshall (National Museum of New Zealand) for information; to Mr A. D'Attilio (Natural History Museum, San Diego) for his suggestions and to Mrs M.L. Buyle (Brussels) for the development of my photographs. Finally I am very thankful to Dr E.H. Vokes (Tulane University) for reading and making suggestions on my manuscript and for her very helpful information.

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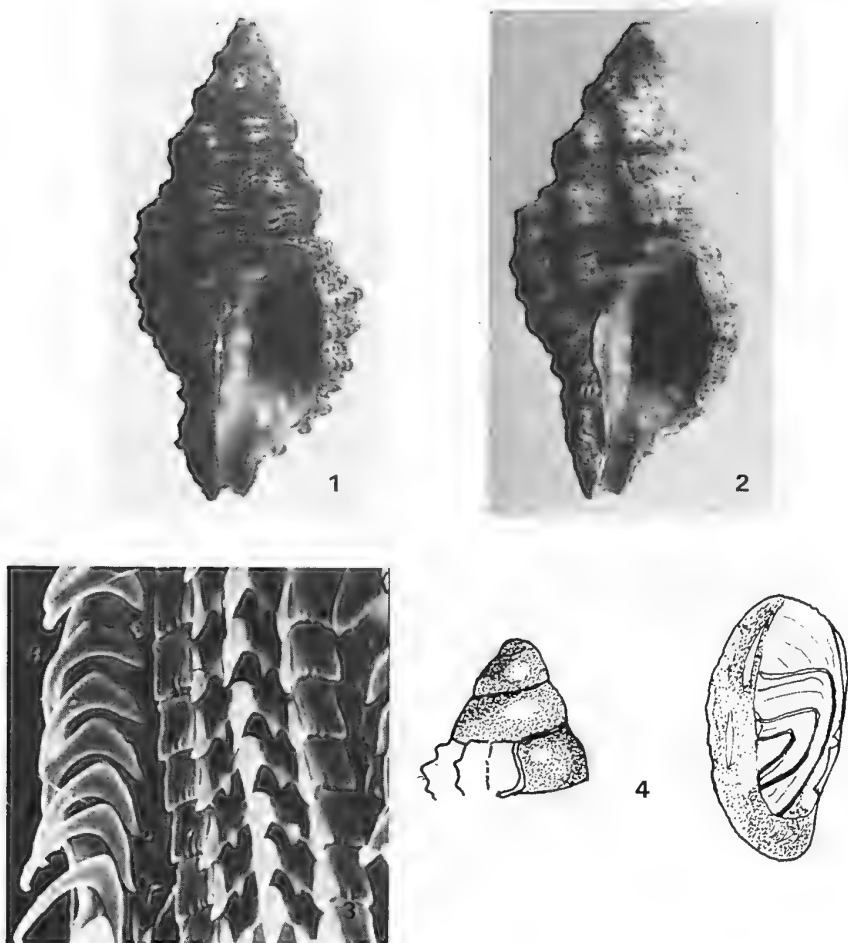


Plate 1: *Orania alexanderi*. Fig. 1: holotype (18.9 x 9.5 mm). Fig. 2: paratype Australian Museum (19 x 9.1 mm). Fig. 3: Scanning micrograph of the radula, MNHN, Paris (x 380). Fig. 4: Protoconch (x 25) and interior (x10) of operculum of *Orania alexanderi*.

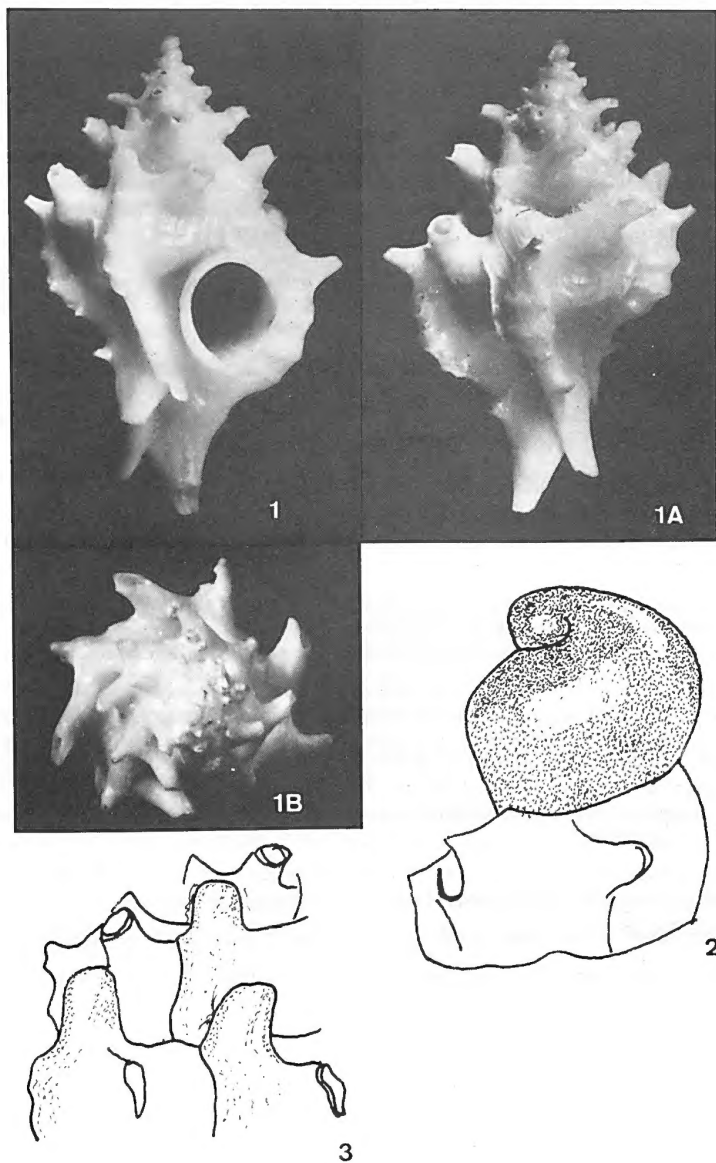


Plate 2: *Typhis wellsi*. Figs. 1-1A-1B: holotype (22 x 14.5 mm). Fig. 2: Protoconch of the holotype (x 35). Fig. 3: Details of varical buttresses (x 6).

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